Life-history traits and potential causes of clutch-size decline in the introduced song thrush (*Turdus philomelos*) in New Zealand

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Summer is coming, summer is coming.
I know it, I know it, I know it.
Light again, leaf again, life again, love again,
Yes, my wild little poet.

-Excerpt from “The Throstle” (Alfred Lord Tennyson);
the rhythm mimics the song thrush’s song

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ABSTRACT

The song thrush (*Turdus philomelos*) was introduced to New Zealand from Britain during the mid 19th century and has become one of the most common terrestrial bird species in New Zealand. In this study, I surveyed a range of life-history traits in New Zealand song thrushes for comparison with traits of British thrushes. Clutch size, egg size and nest size have decreased, while the nestling period is shorter and the incubation period longer. This combination of changes suggests birds are investing less energy into each reproductive bout. Birds also appear unable to raise large broods, as nestling starvation is common in New Zealand, which suggests that food is limiting. I experimentally tested the ability of song thrushes to incubate enlarged clutches and broods, but productivity was not higher for enlarged broods and natural 3- and 4-egg clutches produced similar numbers of fledglings. Thus reduced clutch size may be an adaptation to the local environment. Differences in female incubation behaviour, with 3- and 4-egg clutches receiving higher levels of incubation and more visits per hour than 5-egg clutches, also suggest New Zealand thrushes have difficulty coping with clutches as large as those in Britain.

The decrease in clutch size between New Zealand and Britain is in the direction and magnitude expected based on the change in latitude, which supports the hypothesis that factors affecting foraging time and food availability, such as daylength, temperature and rainfall, may be selecting for smaller clutches. Egg size was also found to have decreased in New Zealand, though this may be the result of smaller adult size. Hatchling mass was related to egg volume, but I found no effect of egg volume or clutch size on hatching success. However, nests containing more pointed eggs (i.e., abnormally-shaped eggs), had lower survival and hatching/fledgling success.

Data from the national nest record database and my study both suggest that differences in song thrush productivity are the result of differential survival of nestlings. Nestling mortality due to starvation was common at Kowhai Bush, but rare in Britain, so either adult condition or food availability may be lowering reproductive success in New Zealand. High rates of nest failure (>65%) could also affect clutch size, but the strong directional selection imposed by food limitation during the nestling period suggests that increases in food supply would result in increased reproductive success even with the same levels of nest failure. When comparing clutch size throughout New Zealand, I found a significant, positive relationship with rainfall, which further suggests that food limitation may be the main factor driving changes in life history traits of song thrushes in New Zealand.

=== Chapter 1 ===

General Introduction

1.1 Life-history traits in changing environments

Under changing environmental conditions, the optimal amount of investment an animal allocates to reproduction over survival, or in each reproductive attempt and individual offspring, is expected to vary and involve trade-offs (Stearns 1992). Those that can take advantage of favourable conditions are more likely to have higher reproductive fitness (i.e., produce more surviving offspring) and therefore the traits they possess should become more widespread in the population. In contrast, if environmental conditions are relatively predictable, individuals can learn – or selection can lead to the development of innate responses – what level of investment will maximise their fitness. For example, avian clutch size, one of the most important fitness-related traits, has been found to vary with food and resource availability (Lack 1947, Martin 1987, Graveland & Drent 1997), and perceived or actual predation risk (Skutch 1949, McNamara *et al.* 2008), among other factors. In long-lived species, tradeoffs between survival and reproduction (i.e., current and future reproduction) have also been shown to influence life history traits and the overall level of investment in each reproductive attempt (Dhondt 2001, Mills *et al.* 2005, Fontaine & Martin 2006).

The ranges of many species span several habitat types, such that individuals of the same species can be exposed to differing environmental conditions; thus, local adaptations may develop to enhance the ability of individuals to exploit local conditions (Gordon *et al.* 2009). Indeed, the link between changing environmental conditions and adaptation has been a major focus for evolutionary biologists (e.g., Reznick *et al.* 1990, Grant and Grant 2002, Garant *et al.* 2004). Currently, human activities are causing environmental change at a faster rate than species may be able to evolve adaptations (Visser 2008). For example, approximately 12% of the world's bird species are threatened with extinction, and habitat change is one of the main drivers (Stattersfield *et al.* 2000). If we could better understand selection on life history traits, and what factors have the greatest effect on fitness and survival, we

could potentially increase the efficacy of conservation measures. Although introduced species are usually ignored by conservation biologists, or viewed as potential problems for native species, they can provide an opportunity to examine the ability of a population to adapt to novel and changing environments. Many bird species have been introduced around the world, and they seldom meet environmental conditions that are exactly the same in the introduced range as in the source range. Thus, species that have been introduced into new regions may provide a useful 'experiment' for testing how species adapt, and the speed at which they can adapt, to new environments.

1.1.1 Examples of rapid evolutionary change

Only in the last hundred years have scientists considered it possible to observe evolution over ecological, as opposed to geological, timeframes. Bumpus (1899) was the first to show natural selection in action when he was given 136 house sparrows (*Passer domesticus*), 64 of which subsequently died, that were caught (by hand) after a severe storm in New York. He found that structurally small birds were more likely to die than larger individuals, which he suggested was evidence for selection for larger body size. Although the sample was biased by its small sample of females and the method of collection (picking up birds that were on the ground), which likely excluded the fittest individuals, later studies using modern statistical analyses on Bumpus' measurements still find a significant difference in body size between survivors and non-survivors (Buttemer 1992).

Nowadays, 'rapid' evolutionary change (within a few hundred years, but often <100 years or 100 generations), or 'contemporary evolution', has been observed or experimentally invoked in many species, and may even be the norm (Hendry & Kinnison 1999, McKay 2009). Evolutionary changes can be measured by comparing changes in the same population over time or differences between two populations with a common ancestry. The latter design measures evolution indirectly, via the 'divergence' of the two populations; the differences are still a result of evolution, but rates of evolution may be faster or slower than the degree of divergence suggests (Hendry and Kinnison 1999). Differences in traits over time may be the result of phenotypic plasticity (learned or environmentally influenced changes in existing phenotypes) and/or underlying genetic changes. Determining the importance of phenotypic vs. genetic factors requires a direct study of genotypes within each

population, but can also be inferred from careful experiments (e.g., rearing individuals in controlled environments, Reznick *et al.* 1990).

Possibly the most well-known avian examples of rapid evolutionary change relate to bill size of Darwin's finches in the Galápagos (Grant & Grant 2006). Bill sizes of the medium ground finch (*Geospiza fortis*) vary according to the size of seed available, which is affected by weather patterns. A drought in the 1970s selected for birds with larger bills, because small seeds were less abundant and more birds with small bills starved. Conversely, after an El Niño event increased rainfall in 1983, small seeds became more plentiful and selection favoured small bills (Boag and Grant 1984). Similarly, when in competition with the large ground finch (*G. magnirostris*), whose larger bill makes it more efficient at handling larger seeds, *G. fortis* bill size decreased via differential survival of small- and large-billed birds (Grant & Grant 2006). Studies on Trinidadian guppies (*Poeciliea reticulata*) have also shown clear and rapid adaptive responses to changing environmental conditions. When predators are present, colour spots on males are small, but in the absence of predators, female preference quickly selects for males to become more colourful (Reznick *et al.* 1990).

1.2. Introduction of alien species

Although invasion is a natural process, human activities have significantly increased rates of introduction of plant and animal species through deliberate and accidental introductions of non-native species into entirely novel environments. This, in combination with wholesale modifications of the existing landscapes/ecosystems, has made an understanding of the effects of introduced species and why some species fail to establish while others succeed, vital for the conservation efforts and survival of many native species. For example, the widespread introduction of exotic mammalian predators has led to the extinction of many native birds in New Zealand. One of the main conservation tools to prevent further losses is to establish new populations on offshore islands with no introduced predators. For such procedures to be successful, understanding why some introductions succeed and others fail is critical.

Two main factors appear to be important in the success or failure of an introduction: the ecology of the species (i.e., species-specific traits), and introduction effort (measured by the number of releases, number of individuals per release and number of release sites, Veltman *et al.* 1996, Duncan

1997). Typically, introductions of generalist species are more successful than specialists (Long 1981) and climate and habitat matching also play a part (Keller & Taylor 2008). Of the 133 bird species introduced to New Zealand, only ~40 are now successfully established (Long 1981). Very few game-birds have successfully established populations in New Zealand, despite considerable effort (>1000 birds introduced over multiple releases throughout the country, Long 1981). In comparison, over a dozen passerine species have become well established, after only 11-800 (mean: 381 ± 226 SD) birds of each species were released. In some cases, these introductions succeeded with even relatively few founders. For example, cirl buntings (*Emberiza cirlus*) have established a small but persistent population in New Zealand's South Island after only 11 birds were introduced. Thomson (1922) suggested that stoats and weasels were responsible for the failure of >20 game-bird species to become established, as well as competition with smaller birds for food. Migratory behaviour often also limits the success of introductions. For example, nightingales (*Daulias luscinia*), blackcaps (*Sylvia atricapilla*), and various migratory species of geese were introduced but failed to establish in New Zealand (Thomson 1922). Interestingly, Thomson (1922) reports that the mallard (*Anas platyrhynchos*) and Canada goose (*Branta canadensis*) were only "partially naturalised", but they have now reached pest proportions and are totally naturalised. The mallard is in fact causing the extinction of the native grey duck (*Anas superciliosa*) through hybridisation (Rhymer & Simberloff 1996).

Maximising individual fitness as well as survival is vital for conservation plans, which typically have limited budgets and are funded by politically-, economically- or socially-driven governments and organisations for whom numbers are often the clearest evidence of success. Introduced species are typically overlooked in conservation plans, but studying how such species have adapted to the new environment, and what impact any changes have had on individual fitness, may provide better methods to promote introduction success of endangered native species and to choose locations that will facilitate the fecundity of new populations, or avoid locations that may depress fecundity.

1.2.1 Introduced species in the New Zealand environment

As a result of British colonists' efforts, much of New Zealand now resembles Britain, with many of the same farming practices creating similar landscapes, while deliberate introductions of both animal and plant species mean that the ecosystems share many of the same species. The New Zealand climate

is also similar to that of Britain; however, the summers tend to be drier and the winters warmer and milder (MacLeod *et al.* 2007). There is still a seasonal pulse of food in the spring, but New Zealand may be less seasonal and breeding seasons may be longer (Evans *et al.* 2005). Many of these climatic differences stem from New Zealand's lower latitude. Compared to Britain, New Zealand is ~10 degrees closer to the Equator and would sit in the equivalent position of Spain in Europe. As a result, daylength is shorter in New Zealand during the summer, but longer in winter. As most species of passerines introduced to New Zealand were sourced from southern England, introduced species have also had to cope with environmental conditions typical of a warmer climate. Indeed, it is tempting to equate the translocation of birds from a colder Britain to a warmer New Zealand as similar to the rapid environmental changes that birds in the native range are expected to face with global warming. Thus, an understanding of how introduced birds in New Zealand have changed relative to that in their native range may provide valuable insight into the adaptability of birds in a warmer world.

1.3 Life-history traits

Life-history traits include all the features – morphological, physiological and behavioural – of an organism affecting its ability to survive and reproduce. Differences in the forms of traits expressed by an individual may be subject to selection, such that individuals displaying a certain form are favoured or selected against, depending on the fitness value of that form in the particular environment. Thus, variation in the environmental factors that influence selection can drive changes in selection pressure, which causes optimal trait values (i.e., those maximising lifetime fecundity) to vary both spatially and temporally (e.g., Charmantier *et al.* 2004, Chamberlain *et al.* 2009, Gordon *et al.* 2009) and can also result in tradeoffs within traits (Roff & Fairbairn 2007, Wang *et al.* 2009). For example, body size in birds has important consequences for both survival and reproduction. Larger (or heavier) individuals are better able to cope with periods of starvation and sudden weather events (e.g., storms or colder temperatures; Murphy 1985), but being heavier increases the costs of flying and also the risk of being caught by a predator (Benkman 1991, Lima 2009), which can select for smaller birds in areas of high predation risk despite the potential reduction in survivorship. Thus, in an unpredictably variable environment, opposing selection pressures, or rapid shifts in the direction of selection, may have such

a negative effect on survival and/or reproduction that individuals are unable to adapt sufficiently rapidly to cope with the changing environmental conditions, so the population will collapse.

With its significant effect on individual fitness, there is likely to be strong selection to optimise clutch size at each reproductive attempt. If a female lays three eggs when she could successfully have produced four surviving offspring, she has immediately reduced her reproductive output by a quarter. In birds with altricial young that depend entirely on their parents for food (and for thermoregulation in their first days/weeks of life), Lack (1947) proposed that food availability (which is also linked to habitat quality and population density) was the main selective force on clutch size. In other words, the optimal, and thus the most common, clutch size should correspond to the number of offspring the parents can successfully raise; that is, the most common clutch size should be the most productive (producing the highest number of fledglings). However, many factors influence reproductive success and most studies have found that many species of birds can raise additional offspring (Skutch 1949, Nur 1986, Godfray *et al.* 1991).

Laying four eggs (and raising four offspring) might affect a female's future survival or offspring-rearing capabilities, or it may reduce the quality of the offspring, which either requires a compensatory increase in subsequent parental investment or gives the offspring a permanent disadvantage (i.e., lower survival). Thus, tradeoffs between current and future reproduction (Martin 2002, de Heij *et al.* 2006), or between offspring condition and number (e.g., Smith *et al.* 1989, Deerenberg *et al.* 1996, Hõrak 2003) may result in the commonest clutch size being less than the most productive clutch size at a single breeding attempt (Engstrand & Bryant 2002, Martin 2002, Dobbs *et al.* 2006).

Nest predation can also select for smaller clutches in several ways (Skutch 1949, Slagsvold 1984) and, in areas of high predation, may even over-ride any effects of food limitation (Fontaine & Martin 2006). Where predation is disproportionately higher on large clutches, selection will favour smaller clutches. If higher activity levels at nests with larger clutches result in these nests being more conspicuous to predators, this could select for fewer visits (i.e., decreased activity) and, in turn, restrict the amount of food brought to the nest and therefore offspring number (Skutch 1949). On the other hand, high levels of nest failure could select for smaller clutches if the nesting period of smaller clutches is shorter than for larger clutches or if reduced investment in each clutch allows for faster recovery and

renesting after a nest fails (Slagsvold 1984). The effects of nest predation can also be seen when comparing species with different nest types. For example, cavity nesters with generally safer nest sites typically lay larger clutches than birds that build more vulnerable open-cup nests (Jetz *et al.* 2008).

There are a number of other factors that have been identified as affecting clutch size. In some situations, there may also be non-adaptive reasons for variation in clutch size. If females are resource-limited during laying, they may be unable to lay an optimal number of eggs (Perrins 1970). Similarly, female condition may influence clutch size, as birds in poor condition may be unable to lay large clutches or lay smaller clutches than females in better condition (Nur 1986, Monaghan & Nager 1997, Wilkin *et al.* 2006). Mode of development and phylogeny can also affect clutch size as over half of all bird species lay 2-3 eggs per clutch, suggesting some phylogenetic conservativenes, and altricial species have smaller clutches than precocial species (Jetz *et al.* 2008), suggesting the level of post-hatching parental care affects clutch size.

In many species, seasonal decreases in clutch size are common (Perrins 1970, Cooper *et al.* 2005), though some species show an initial increase in clutch size before the decline (e.g., great tits *Parus major*, Perrins 1970). The reasons for seasonal patterns are not well understood. For song thrushes, it is likely that food availability decreases over the season, as earthworms – the main food provided to nestlings (Gruar *et al.* 2003) – travel deeper into the soil as the topsoil dries out and are therefore less accessible to birds (Gerard 1967). It is also possible that the probability of survival to breeding is lower for late-season fledglings (e.g., this is the case for great tits, Perrins 1970, and house wrens *Troglodytes aedon*, Styrsky *et al.* 2000), which would lower the value of these fledglings in terms of parental fitness. Geographic and latitudinal differences in clutch size are also common; for example, species on islands, in the Southern Hemisphere, and those closer to the Equator tend to lay smaller clutches (Martin 1996, Jetz *et al.* 2008). Despite many studies, the exact causes of these patterns are still unclear, as predation rates and competition often explain clutch-size patterns within, but not between, geographic regions (Martin *et al*. 2000).

1.4 Clutch size

Mean clutch size of several introduced passerine species appears to have decreased in New Zealand (Evans *et al.* 2005); however, no detailed studies have been undertaken to explain this decline. Song

thrushes (*Turdus philomelos*) lay 4-5 eggs per clutch in Britain, but only 3-4 eggs per clutch in New Zealand (Chapter 2). Clutches of five eggs do occur, but they are uncommon (Chapter 3); if the reason for their rarity is because most birds cannot raise five young, then experimentally-enlarged clutches will not be more productive (Lack 1947). Papers on clutch and brood manipulation experiments are common in the literature, but there is still value in using the procedure on different species or populations, as our understanding of clutch-size evolution is still incomplete. None of these studies has been conducted on introduced populations of birds, in which it is known that clutch size has changed within the historic period. Moreover, intraspecific studies may be useful for teasing apart the reasons for variation in clutch size, because fewer variables may be involved.

1.5 Egg size and fitness

Variation in egg size is more subtle than differences in clutch size, but it too reflects the level of initial investment by the female and may be just as important for parental fitness if egg size and/or composition affects hatching success or offspring quality (Potti & Merino 1996). Small eggs may be less likely to hatch (e.g., Amundsen *et al.* 1996, Simmons 1997, Serrano *et al.* 2005) and abnormally-shaped eggs may also have reduced hatching success (Narushin & Romanov 2002), though not all studies find such relationships (e.g., Encabo *et al.* 2001). Intraspecific studies have found that larger eggs produce larger nestlings, even within clutches, but the relationship between egg size and nestling size typically disappears over the course of the nestling period (Smith *et al.* 1995, Amundsen *et al.* 1996, Christians 2002, Krist *et al.* 2004), or was never significant (Williams 1994). Thus, the benefits of hatching from a larger egg are still unclear and may be correlated with female quality (Hõrak *et al.* 1997, Potti 1999). Where it has been studied, the costs of egg production have been found to be as important as the costs of incubation and feeding nestlings (Monaghan & Nager 1997, Martin 2002, Pérez *et al.* 2008), and high quality females may be able to lay optimally-sized/shaped eggs as well as provide sufficient nutrition post-hatching. For example, Potti (1999) found that female pied flycatchers (*Ficedula hypoleuca*) in better condition – both as nestlings near fledging and as adults – laid larger eggs. The connection between egg size and female quality is sufficiently strong that some studies have even used egg size as a proxy for female quality (e.g., Risch & Rohwer 2000), although this may not necessarily be true or consistent for all measures of quality/condition (Potti & Merino 1996).

Egg size is highly heritable and repeatable within individuals (Christians 2002), yet several species show observable patterns in egg size, such as increasing or decreasing size of eggs with laying order (Slagsvold *et al.* 1984, Potti & Merino 1996, Viñuela 1997). The reason for these patterns is not always clear, and it is not necessarily adaptive (Magrath 1991, Potti & Merino 1996, Bitton *et al.* 2006), but may be related to enhancing nestling survival or reducing competition amongst siblings. For example, when incubation is begun before clutch completion, laying larger eggs later in the laying order may at least partially mitigate the negative effect of asynchronous hatching, because although nestlings that hatched first have an advantage over their younger siblings, the younger ones are larger as hatchlings (Soma *et al.* 2007, Maddox & Weatherhead 2008). Female condition and maternal effects have also been found to influence both egg size and offspring condition (Potti 1999), while tradeoffs between clutch size and egg size or hatching success may also moderate selection on both clutch size and egg size. For example, Potti & Merino (1996) found a significant decrease in hatching success with increasing clutch size for fertile, unhatched eggs in the pied flycatcher. If female condition is related to egg size, clutches of small eggs may be more frequently abandoned than clutches of large eggs.

Eggs of introduced species appear to be smaller in New Zealand than in their native range; Congdon & Briskie (2010) found a 5.5% decrease in egg volume and a 2.2% increase in the elongation of eggs (i.e., eggs in New Zealand are relatively more pointed than those in Britain). However, the fitness effects of this difference is unknown. Williams (2001) used chemical injections to experimentally reduce the size of captive zebra finch (*Taeniopygia guttata*) eggs by 8%, which caused reduced hatching success but had no effect on offspring fitness. A later study, in which females were given higher doses, induced a decrease of 18% and this was sufficient to significantly reduce both hatching success and offspring condition (Wagner & Williams 2007). Thus, the degree of change that has occurred in New Zealand may not be sufficient to affect individual fitness. However, smaller changes in egg size might have fitness consequences for wild birds that may not be expressed in captive animals with unlimited food and constant environmental conditions. Decreases in egg size may reflect changes in female body size/condition, resource limitation (e.g., calcium levels: Mänd & Tilgar 2003, Wilkin *et al.* 2006), or energetic constraints during the laying period (Magrath 1991, Krist *et al.* 2004). But if the changes in egg morphology have a negative effect on hatching success and/or nestling

condition, birds may also be paying these costs in terms of reproductive success. Alternatively, selection favouring reduced investment in each reproductive bout could make laying slightly smaller eggs adaptive. If birds are living longer in New Zealand, it is likely to affect tradeoffs between current and future reproduction (Stearns 1992). It is also possible that birds are being selected to reduce investment specifically in the first stages of breeding. For example, high rates of nest failure during egg laying and incubation could select for smaller eggs (Slagsvold 1984, Fontaine & Martin 2006).

1.6 Aim of thesis

Apart from descriptive studies of clutch size and egg size, few studies have examined changes in life-history traits among introduced birds in New Zealand. For most life-history traits, it is not known whether any changes have occurred nor what effect these changes may have on breeding success and fitness. Genetic differences between the introduced and native ranges of most species are either poorly studied or completely unknown except for a few species in which it has been found that there is less genetic diversity present in the New Zealand populations, perhaps as a result of passing through bottlenecks during their establishment (Merilä *et al.* 1996). There is also some evidence that body mass and morphology have changed among a number of introduced species in New Zealand (Debruyne 2008), but how this may have affected life-history strategies is not known. Differences in food supply between New Zealand and Britain are also unknown, but as many parts of New Zealand have much lower rainfall over the breeding season than in Britain, this may reduce the availability of invertebrate food for nestlings, which could select for changes in reproductive strategies, such as smaller clutches or fewer broods per year (Martin 1987).

There are also few studies of rate of nest predation on introduced species and how this compares to that in the native range, although MacLeod *et al.* (2005) found no significant difference for introduced yellowhammers (*Emberiza citrinella*) in New Zealand. Not surprisingly, the warmer climate in New Zealand has led to an increase in the length of the breeding season (Evans *et al.* 2005) and birds may also be living longer (J. Briskie, pers. comm.), both of which could have an important effect on the tradeoff between current and future reproduction and the optimal level of investment in reproduction over survival (Stearns 1992). The objective of my thesis is to examine changes in life-history traits and their potential fitness effects, using the song thrush as a model system.

1.7 The song thrush

Song thrushes are native to continental Europe and the United Kingdom and were introduced to New Zealand from England in the mid-late 1860s and early 1870s (Thomson 1922). During this time, a total of ~400 individuals were released by Acclimatisation Societies in New Zealand's main centres (Table 1.1). Within ~65 years, song thrushes were present throughout the country (Long 1981). Their current distribution spans the whole of New Zealand, including offshore islands, though they are less abundant in dense forests and rare or absent in alpine regions (Robertson *et al.* 2007). They are now one of the most common terrestrial bird species in New Zealand (Spurr 2008) and are in fact considerably more abundant in New Zealand than in Britain, though the reason is not clear. Approximately 17% of the New Zealand native flora produces fruits, compared with ~5% in Britain (Thomson 1922), so it is possible that food supply is greater in New Zealand (for adults; nestlings are fed invertebrates). It is not thought that thrushes pose a threat to any native bird species, but horticulturalists see them as pests because they damage fruit crops. They are omnivores and eat a wide range of invertebrates as well as berries and fruit, utilising both native and exotic food sources (Heather & Robertson 2000). Song thrushes have also become established in the bird fauna of various islands in the Pacific (e.g., Norfolk Island) and Australia, where thrushes have only established in Melbourne, despite being introduced into several areas. Attempts to introduce song thrushes to South Africa and America were unsuccessful (Long 1981). In Britain, song thrush numbers have declined sharply in the past 50 years. Low juvenile survival during their first winter (Robinson *et al.* 2004), loss of grassland habitat and increasing uptake of agricultural practices that promote the drying out of the top soil (Peach *et al.* 2004) are thought to be responsible for the decline. Elsewhere, numbers appear stable (Cramp 1988).

A medium-sized (70-80 g) passerine, the song thrush is socially monogamous, though the extent of extra-pair paternity is unknown. Males are generally slightly larger than females, but otherwise their plumage is indistinguishable (brown upper parts with a brown-speckled white breast) and females can only be identified during the breeding season by their brood patches. Pairs establish territories (~20 m^2 up to ~3 ha) in late winter and the female builds the nest, usually in a tree or shrub; in cities, some also use walls and buildings. Incubation is carried out by the female and is usually begun after the last egg is laid. Some females begin incubating after the penultimate egg is laid, which leads to the last egg

hatching several hours after its nestmates; otherwise hatching is synchronous. Males rarely feed the female while she incubates, but such behaviour is not unknown (pers. obs.). Both parents provide food for the nestlings, typically feeding them earthworms, but as the ground dries out and earthworms become less accessible, they also bring them other invertebrates, such as spiders, beetles and flies. At fledging, offspring are fed by their parents for up to three weeks (Cramp 1988, Heather & Robertson 2000), before dispersing away from their natal site. The species encompasses both migratory and non-migratory populations, with those at lower latitudes being partially or entirely sedentary (Cramp 1988). There is no evidence of migratory behaviour in New Zealand.

The genetics of song thrushes have not been studied in New Zealand, but inbreeding depression is not likely to be an issue, as >150 individuals were released in total (Briskie & Macintosh 2004). Thus, any changes in life-history traits must either be an adaptive response to the New Zealand environment, or a reflection of constraints imposed by differences between New Zealand and Britain. Although each release typically comprised of <50 birds (Table 1.1), 282 birds were released in 1867-68, compared with only 6 in 1865-66, so if there was any period in which rates of inbreeding were higher than normal, it was most likely limited to the breeding season of 1866 (when first-year breeders joined the breeding population). Thomson (1922) reported apparently high numbers of albino thrushes in New Zealand, which could point to increased rates of genetic abnormalities than in Britain, but he thought the numbers were not increasing, so either albinism was not higher than in Britain, or the more inbred (albino) individuals had lower fitness and were 'bred out' of the population.

1.7.1 New Zealand study site: Kowhai Bush

The bulk of the data presented in this thesis comes from a population of song thrushes at Kowhai Bush, Kaikoura (42º23'S, 173º37'E, New Zealand Geodetic Datum 1949). This 240-ha forest lies on the floodplain of the Kowhai River (Fig. 1.1), a fact which saved it from total conversion to pasture and also resulted in sections of the forest being at varying stages of succession. It is surrounded by farmland (primarily diary farms) and officially became a protected area in the late 1970s, at which time large grazing animals were excluded. There are occasional poison drops targeted at brushtail possums (*Trichosurus vulpecula*), but no other pest or weed eradication measures are in place. Cats (*Felix catus*), rats (*Rattus* spp.) and stoats (*Mustela ermina*) are the main avian predators and pose a

threat to both adults and nests. The forest is also inhabited by other mammals, such as hares (*Lepus capensis*), and other introduced birds, such as blackbirds, with whom song thrushes may compete for territories and food, although this has not been studied. Introduced invertebrates provide prey of many of the same species that song thrushes evolved to exploit in their native ranges, including introduced European species of lumbricid earthworms and common garden snails (*Cantareus asperses*).

On the younger, least-developed soils, where song thrushes are more abundant, the canopy is dominated by kanuka (*Kunzea ericoides*) and the forest floor by *Sphagnum* moss. Introduced plants, such as barberry (*Berberis glaucocarpa*), broom (*Cytisus scoparius*) and gorse (*Ulex europaeus*) are also present in these areas and provide additional nesting locations for both native and introduced birds; barberry fruits also provide a food source (Thomson 1922). The older areas of forest are floristically more diverse and have a much higher canopy, but while blackbirds are just as common in these areas, song thrushes prefer to nest in the younger, more open-canopied forest (pers. obs.). This type of forest is structurally similar to the woodland habitats of Britain although the species of trees differ. Thus, I focused my efforts on the younger areas, searching most intensively for nests within a 15-20-ha area of the forest (Fig. 1.1).

Overall, Kowhai Bush appears to be a good quality habitat, as the number of pairs (occupied territories) is high for many native and introduced species of passerine, and research on various species has been carried out there since the 1970s (Hunt & Gill 1979). There are eight species of native birds living and breeding in Kowhai Bush, as well as eleven species of introduced birds, including song thrushes. Nevertheless, food supply for some species like the song thrush may decrease rapidly over the breeding season. Rainfall is low throughout the year, and even in years of high winter rainfall, such as 2008, when >500 mm of rain fell (240 mm is more typical, Table 1.2), the soil appears to dry out rapidly, so earthworms will quickly become less accessible. In 2008, large pools of excess water built up in areas of older forest (where the soil is more developed), but even these had all disappeared by mid-November. Compared with southern England, the habitat at Kowhai Bush appears to be drier, sunnier, and warmer (Table 1.2). Frosts do occur at Kowhai Bush during spring, but snow even in winter is rare.

1.8 Outline of thesis

This thesis is broadly divided into two sections. In the first half, I compared life-history traits among different populations, while the second half is focussed on fitness consequences of two life-history traits that were known to have changed in the introduced population. The final data chapter contains experimental data, while the previous chapters rely on data from observations in the field.

Chapter 2 reports the results a general survey of life-history traits in the song thrush. The objective of this chapter was to compare a variety of life-history traits of song thrushes in their introduced range in New Zealand with the British source populations, in order to assess the extent of change that has occurred since their introduction.

In Chapter 3, I used the national nest record database to gather sufficient data on clutch size, number of eggs hatched, and number of nestlings fledged across New Zealand. I then compared variation in these traits with latitude, geographic region and climatic variables (mean annual rainfall, temperature, and hours of sunshine) within New Zealand. I also tested the relationship between latitude (relative distance from the Equator) and clutch size across the global range of latitudes the song thrush inhabits.

As clutch size and egg volume are known to have decreased in both song thrushes and other introduced birds in New Zealand (Evans *et al.* 2005, Congdon & Briskie 2010), in the second half of my thesis I examined the potential fitness consequences of these decreases. Chapter 4 focuses on egg volume, shape and mass and whether these traits affect hatching success and nestling size and mortality. As egg size and clutch size may be related, this was an opportunity to test for a tradeoff, as well as determine the possible fitness benefits of hatching from larger eggs.

Because clutch size is one of the key life-history traits, having a significant effect on fecundity (Godfray *et al.* 1991), I was particularly interested in finding a potential cause for this decline. One obvious explanation might be that the change in environmental conditions between Britain and New Zealand meant thrushes could no longer feed broods of the ancestral size; thus selection may have favoured a reduction in clutch size to more closely match the ability of parents to feed their brood (Lack 1947). To test this hypothesis, I experimentally manipulated clutch and brood size and recorded the effect of increasing the number of eggs or nestlings on parental behaviour (incubation attentiveness

and feeding rates) and the condition of the eggs (using hatching success) or nestlings (using body size and growth rates). The results are presented in Chapter 5.

Finally, I have brought together my results and conclusions in Chapter 6, the general discussion. In this study, I am not attempting to distinguish genetic variation from plastic responses to environmental pressures, but I was able to show that selection does appear to be acting against larger clutches. The main areas that would benefit from future study are also outlined here.

1.9 References

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Table 1.1. Numbers, locations and release dates of song thrushes throughout New Zealand, as recorded in Acclimatisation Societies' minutes (summarised from Thomson 1922). The Nelson and Canterbury releases were not successful and either these birds died or initially dispersed away from those townships, before the population grew and immigrants arrived in these regions (this process took >20 years in Canterbury). Immediate establishment was noted in Otago and Auckland. "?" indicates releases where the exact number was not recorded.

Location	Year of release	Number released (total)
Otago	1865, 1867-1869, 1871	2, 4, 49, 48, 42 (145)
Auckland	1867-1868	30, 95 (125)
Canterbury	1867-1868, 1871, 1875	36, 24, ?, ? (>80)
Nelson	1872	5
Wellington	1878	8

Table 1.2. Comparison of the climate at Kaikoura, New Zealand (NIWA 2009), with southern England (Met Office 2009).

Climate variables		**Kaikoura, NZ**	**Southern England**
Mean rainfall	Summer	160 mm	150-200 mm
	Winter	240 mm	250-400 mm
Number of days with rain	Summer	20	25-30
(≥1 mm)	Winter	24	35-50
Mean temperature	Summer	15-16°C	14-17°C
	Winter	8-9°C	3-6°C
Sunshine hours	Summer	640	550-700
	Winter	400	170-200

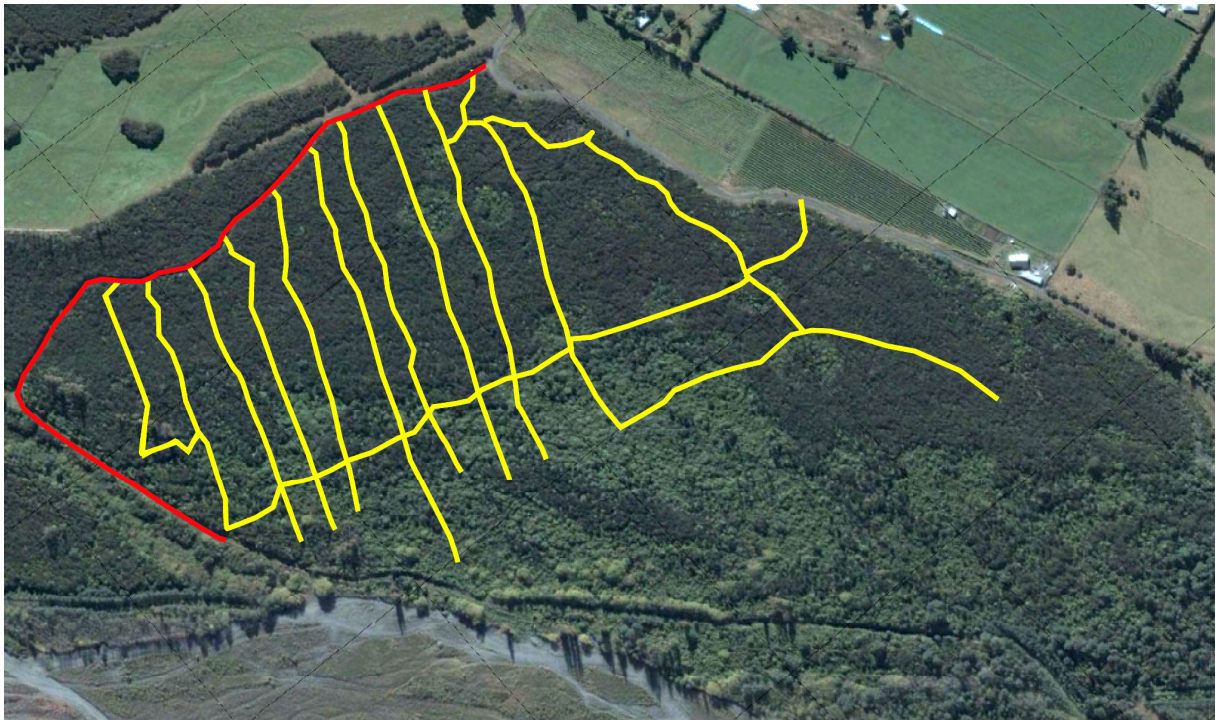

Figure 1.1. An aerial view of Kowhai Bush (42º23'S, 173º37'E) showing the main trails (yellow) and the unsealed, public road (red). North is toward the top of the photo, and the parallel trails (~50 m apart) run approximately north to south. The area of most intensive nest searching is contained within the trails and either side of the road. Some birds that nest <5 m from the road abandon the nest as a result of the disturbance from vehicles and people walking or biking past (some of whom bring pet dogs with them), but the traffic volume is very low. The location of the coastal Kaikoura township within New Zealand is shown in Fig. 3.1 (Chapter 3); Kowhai Bush is 7 km inland from Kaikoura. Aerial photograph © Google 2009.

=== Chapter 2 ===

Life-history traits of song thrushes (*Turdus philomelos*) in New Zealand

2.1 Abstract

The song thrush (*Turdus philomelos*) was introduced to New Zealand from Britain almost 150 years ago. It is now one of the most abundant terrestrial bird species in New Zealand, but little is known about the life-history traits of this species in its introduced range. A variety of life-history traits of a song thrush population at Kaikoura, New Zealand, were studied over a 6-year period and compared with published data from British populations to determine whether changes in life-history traits have occurred since their introduction to New Zealand. Clutch size has decreased in the introduced population from ~4 eggs to ~3.5 eggs, which concords with similar studies on song thrushes and other introduced passerines in New Zealand. Egg size, nest size, nestling period length and breeding success have also decreased significantly in the New Zealand song thrush population, while the incubation period has lengthened. Overall, I found changes between New Zealand and Britain in 8 out of 10 life-history traits sampled. The general 'negative' direction of the majority of these changes suggests that song thrushes in New Zealand are investing less in each reproductive bout than in the native range. As the New Zealand climate is broadly similar to the seasonal conditions in Britain, these changes in life-history traits may be the result of other environmental factors which differ between these Northern and Southern Hemisphere countries. Future research focussing on causes for the observed changes may provide insight into how species adapt to new environments.

2.2 Introduction

The environment in which a species lives is thought to drive selection on its life-history traits in ways that maximise individual fitness (Stearns 1992). Species living in similar environments and occupying similar niches might therefore be expected to exhibit similar life-history traits, creating observable patterns of variation in life-history traits across environmental gradients, as well as between different life-history strategies (Stearns 1992, Begon *et al.* 1996, Paradis *et al.* 2000). Differences between traits of Northern and Southern Hemisphere species provide one such intriguing pattern. Although Southern Hemisphere bird species have been studied less than their Northern Hemisphere counterparts, they have been found to display distinctive variations in life-history traits, such as lower clutch sizes (Martin 1996). Why these traits differ is not clear, but Northern Hemisphere species that have been introduced and become established in the Southern Hemisphere provide an interesting natural 'experiment' for understanding the evolution of life-history traits at the global scale. In other words, by studying the life-history traits of species that have become established outside their natural range, one might be able to link changes in life history with differences in the environment between native and introduced ranges.

The song thrush (*Turdus philomelos*) is a medium-sized passerine that was introduced to New Zealand from Britain over a period of ~15 years in the mid-19th century (Thomson 1922, Long 1981). Acclimatisation Societies carried out a series of introductions at each main city in New Zealand, leaving detailed records of numbers and locations. It is thought that about 400 thrushes were released in New Zealand and the species is now widely established throughout the country. It is particularly common in farmland, native forest (but not dense forest) and urban areas (Robertson *et al.* 2007), where many of the species song thrushes encounter are ones also present in Britain. For example, introduced invertebrate species, such as lumbricid earthworms and the brown garden snail *Cantareus asperses*, provide familiar prey, while introduced mammalian predators (primarily rats *Rattus* spp. and stoats *Mustela ermina*) may cause similar rates of nest predation (e.g., MacLeod *et al.* 2005 found no difference in nest predation between New Zealand and Britain for another introduced European bird, the yellowhammer *Emberiza citrinella*). On the other hand, thrushes in New Zealand exploit native plants for nesting (e.g., kanuka *Kunzea ericoides*) and feed on native fruits (e.g., *Coprosma* spp.). Hence, the ecosystems New Zealand song thrushes inhabit are broadly similar to those experienced by

their British counterparts but at the same time, they include novel elements from the native flora and fauna.

The physical environment in New Zealand is also broadly similar to that in Britain; the two land masses are similar in size and span similar, temperate latitudes and also experience similar seasonal patterns. However, New Zealand summers tend to be warmer and drier and the winters milder (MacLeod *et al.* 2007), and New Zealand is closer to the Equator than Britain. If transposed onto the Northern Hemisphere, New Zealand would lie at a position similar to that of France and the Iberian Peninsula. Perhaps because of this difference in climate, Evans *et al.* (2005) found that the breeding season of song thrushes was significantly longer in New Zealand compared to Britain (164·5 days vs. 116·0 days), which may enable birds in New Zealand to raise more broods per season than their British counterparts.

Life-history traits might be expected to be the product of long periods of evolutionary adaptation to local conditions, so changes in such traits may not have yet occurred in populations established only within the historical period. Nonetheless, changes in life history traits have already been found in other studies, suggesting either rapid evolutionary change or plastic responses to local conditions. For example, mean clutch size is significantly lower in some birds introduced to New Zealand (Evans *et al.* 2005), and mean egg volume has also decreased significantly (Cassey *et al.* 2005, Congdon & Briskie 2010). This combination of smaller clutches and smaller eggs in New Zealand suggests that females may be decreasing their overall investment in each reproductive bout, but data on other life-history traits are scarce. Here, I present a comparative analysis of life-history traits of song thrushes between their native (British) and introduced (New Zealand) ranges. The traits surveyed were: clutch size; egg size and morphology; incubation and nestling period duration; nest success; daily nest survival and predation rates; number of broods per year; nest size and nest location. As published data were unavailable for some traits, I also compared data from locations in the native European range other than Britain. These comparisons provide an assessment of the life-history traits of New Zealand song thrushes and how they may differ from their ancestral populations.

2.3 Methods

2.3.1 The study species

The song thrush is a medium-sized (70 g) passerine bird. It builds a large, open-cup nest in trees and shrubs, typically in the fork of two branches. The nest is built primarily of small twigs with grass, skeletal leaves or mosses draped on the outer surface of the nest, and an inner lining of mud or rotted wood fragments mixed with saliva. Intraspecific parasitism is rare (Moskát *et al.* 2003), so I assumed that eggs from a single nest were laid by the same female. The female builds the nest alone and is also the sole incubator. Both parents provision the nestlings, with the male providing the bulk of the food (Hill *et al.* 1999), while the female also broods the young. After fledging, offspring are fed by their parents for a few days, before they disperse from their natal site. New Zealand thrushes are the descendants of birds caught in port cities in southern Britain; these populations of song thrushes are primarily non-migratory; however, birds from central and eastern Europe over-winter in southern Britain (Cramp 1988), and it is possible that some European birds may have been among those collected and released in New Zealand. However, there is no evidence of migratory populations in the New Zealand range.

2.3.2 Data collection

From 2006-2008 I collected data on a range of life-history traits associated with breeding in a song thrush population at Kowhai Bush, Kaikoura (42º23'S, 173º37'E), a 240-ha forest on the floodplain of the Kowhai River. The forest is dominated by kanuka in the younger, least-developed soils, where song thrushes are most abundant. The forest, which is bordered by farmland, has been fenced off from grazing animals since the late 1970s, but introduced hares (*Lepus capensis*), possums (*Trichosurus vulpecula*), hedgehogs (*Erinaceus europaeus*), stoats, cats (*Felis catus*), rats and mice (*Mus musculus*) are still present. Nest monitoring of song thrushes and other species has been carried out in a section of this forest since 1998 (J. Briskie, unpubl. data), so for several traits I was also able to include data from pre-2006 nests.

Ten life-history traits associated with breeding were included in this study. Clutch size was defined as the number of eggs laid per nesting attempt and confirmed when the same number of eggs was present for two consecutive visits during incubation, or if the visits were < 9 days apart and the

eggs had hatched by the second visit (which confirmed that incubation was underway on the first visit). Eggs from a subset of nests were measured (length and maximum width) using digital callipers (accurate to the nearest 0.01 mm) to estimate volume, using the formula 0.5 x length x width^2 (after Hoyt 1979), and shape (length:width ratio). Those eggs that were within a day of being laid or incubation onset were weighed with a digital scale (to the nearest 0.01 g) to collect data on fresh mass. Incubation period duration (counted from the day the last egg was laid until the day the last egg hatched) and nestling period duration (counted from the day the first egg hatched until the day the last nestling fledged) were measured to the nearest day. Hatching success (the proportion of eggs that hatched out of the total number of eggs present at hatching) was also recorded for nests where clutch and brood size were known (i.e., not including eggs that were abandoned or predated during the incubation period) and data on brood reduction (mortality of individual nestlings within a nest) was gathered from successful nests where brood size and the number of fledglings were known.

Nesting attempts were classed as successful if at least one nestling fledged, while breeding success was defined as the proportion of eggs in each nest that produced fledglings. Daily nest survival was calculated using the Mayfield method (Mayfield 1961, 1975), whereby the probability of a nest surviving for one day was determined by calculating daily nest failure rates, counted as the number of nests which failed out of the total number of "exposure days" (i.e., the time span of observations). Nest predation and abandonment were also recorded in order to compare the causes of failure between this population and British populations. When nests were no longer active, nest size (mean inner and outer diameter and inner and outer depth) was measured to the nearest 0.1 cm. These dimensions were used to calculate outer nest volume using the formula for a cylinder (the outer shape of most nests was roughly cylindrical), while inner nest volume (typically spherical) was approximated by halving the value obtained from the formula for a sphere:

Nest Volume (outer) = л (diameter/2)^2 height

Nest Volume (inner) = 2/3 л radius^3

Estimates of inner and outer nest volume were also used to calculate the inner:outer volume ratio. These different measures of nest size were used to compare nest volume of different clutch sizes. Nest height and tree height were also estimated visually. Pairs were not leg-banded, so the number of broods per year was estimated using clutch initiation dates over the season. Data on life-history traits

of British (source) populations were taken from the literature, except egg size, for which I had measurements of 30 clutches from the collection at the British Museum (Congdon & Briskie 2010).

Nest searching was most intensively undertaken in a 15-ha area within the forest and primarily consisted of searching vegetation for nests; nests were also located via hearing song thrush alarm calls (which are a possible indicator of proximity to a nest), or when a female was flushed from the nest (this was avoided if possible, in order to minimise disturbance and nest desertion). The majority of nests were monitored from discovery until the nest either succeeded (fledging at least one chick) or failed (nest abandonment or the total loss of eggs or nestlings as a result of predation, poor nest construction, or severe weather events). The final outcome (i.e., nest success) for 57 of 416 nests was unknown or inconclusive and these were omitted from statistical analyses of nest success and breeding success. As these nests were aggregated at the end of the breeding season, nest success may be overestimated for the entire breeding season, or underestimated for late-season success. In other words, nests at the end of the study that failed were recorded as failures in the dataset, while the outcome of nests that were still active was unknown, which may have biased my estimate of raw nest success. However, I have also used the Mayfield method of calculating nest success, which takes information from all nests monitored for at least one day, to provide a better estimate of the actual probability of success. Nests were revisited every two to three days, in order to follow nest progress as accurately as possible while limiting disturbance. Visits were typically made daily as laying, hatching and fledging approached, to determine the onset of laying and the length of the incubation and fledging periods. Nests were most closely monitored in 2006-2008, but there was year-to-year variation in the number of nests found in each breeding season (Table 2.1) that may reflect both the efficacy of search effort and the number of nesting attempts made in that year.

To estimate productivity of song thrushes, I used the equation given by Paradis *et al.* (2000) to calculate reproductive output per attempt (ROA): $BS(DSE)^{IT}(DSN)^{NT}$, where BS is the brood size, DSE and DSN the daily nest survival rates for the egg and nestling stages and IT/NT the length of the incubation/nestling periods. This measure takes into account both nest survival and number of young fledged and thus provides a measure of the number of young produced per year.

2.3.3 Statistical analyses

Statistical tests were carried out using R 2.4.0 (R Development Core Team 2006) and data analysed with generalised linear models (GLMs; Crawley 2005) to analyse trends within the population at Kowhai Bush and t-tests to compare the Kowhai Bush data with data from British populations. All variables and their interactions were initially included in the model, then non-significant variables were successively removed until only significant variables remained, to develop a minimal adequate model (MAM). Egg volume, egg shape, incubation period and inner and outer nest volume were log-transformed to meet the assumptions of these tests. Nest success was tested using GLMs with the distribution specified as binomial (success 1, failure 0), so the appropriate transformation was performed within the test itself and significance tested using the chi-square distribution. Number of hatchlings, fledglings and hatching success were tested using GLMs assuming a quasi-Poisson distribution (the procedure for dealing with overdispersed count data in R) and I used t-tests to compare means between New Zealand and British populations. As the effects of clutch size were not necessarily expected to conform to a linear relationship with the variables tested, I treated it as a factor in all tests. All means are given ± standard error (SE).

2.4 Results

Of 359 nests with known outcomes from the 2002-2008 breeding seasons, 126 were successful (35.1%). The MAM for nest success at Kowhai Bush included year (i.e., between breeding seasons) and month of first egg (i.e., timing of nesting attempts within the breeding season); the number of successful nests differed significantly between years ($\chi^2 = 5.91$, df = 1, 357, $p < 0.05$) and months ($\chi^2 = 18.76$, df = 1, 356, $p < 0.01$). The relationship between nest success and clutch size was not quite significant in this model ($\chi^2 = 6.39$, df = 3, 314, $p = 0.09$), but there was a trend for highest success in 3- and 4-egg clutches and lowest for 2- and 5-egg clutches.

Breeding at Kowhai Bush typically began in mid-September and extended to mid-late December. Data were most intensively collected in 2006-2008 and in these years, first-egg date was September 21, September 19 and September 13, respectively. In earlier years, first-egg date was also between this range except for 2003, when first-egg date for one nest was estimated to be ~29 August. The last first-egg date varied between December 5 and December 15. Approximately 50% of all

clutches found were laid in October and ~30% in November. As the time required for completing a breeding attempt from laying to fledging required ~31 days, the breeding season was sufficiently long enough for 2-3 broods per year, as clutch-initiation dates show (Fig. 2.1). In Britain, the breeding season is of similar length, extending from April to July (with some beginning in March) and birds also make 2-3 breeding attempts per year (Cramp 1988); ~70% of all nests found were started in April and the first half of May (Silva 1949). Evans *et al.* (2005) used the difference between the 1% and 99% quantiles of first egg dates (from the nest record schemes of each country) to calculate the length of the breeding season in New Zealand and Britain, which were 164·5 and 116·0 days, respectively. Using this method for my data from Kowhai Bush, I calculated a value of ~105 days, which is lower than their calculated value for all of New Zealand, but comparable with the value for Britain.

Mean clutch size at Kowhai Bush was 3.56 eggs ± 0.032 (n = 367, range 2-5), which was significantly lower than in Britain (Table 2.2; $t = -36.1$, $df = 366$, $p < 0.01$). This value was also significantly lower than the mean of 3.74 calculated by Evans *et al.* (2005) using nest records from the whole of New Zealand ($t = -5.73$, $df = 366$, $p < 0.01$), although both my estimate and that of Evans *et al.* (2005) indicate clutch size is about one egg smaller in New Zealand than in Britain. There was a significant difference between months ($F = 32.5$, $df = 1, 365$, $p < 0.01$), with clutch size decreasing over the breeding season at Kowhai Bush, as it does in Britain (Fig. 2.2), although it appears clutch size declines faster over the season in New Zealand than in Britain.

Mean egg volume, calculated using the mean volume within each of 154 nests, was 5.60 cm^3 ± 0.039 and mean egg shape (L/W) was 1.325 ± 0.0050. There was no relationship between egg volume and clutch size ($F = 0.56$, $df = 3, 136$, $p = 0.64$), but egg volume increased significantly as the season progressed (month of first egg vs. volume, $F = 7.80$, $df = 1, 151$, $p < 0.01$) and there was a significant difference in volume between eggs from New Zealand and Britain (Table 2.2; $t = -10.7$, $df = 154$, $p < 0.01$). Mean egg shape was not significantly different between clutch sizes ($F = 0.71$, $df = 3, 136$, $p = 0.55$), but eggs from New Zealand were relatively shorter and wider than British eggs, and this difference was significant (Table 2.2; $t = 5.60$, $df = 154$, $p < 0.01$).

The mean number of hatchlings was 3.23 ± 0.057 (n = 209 nests that survived to hatching). There was a significant decrease in the number of hatchlings per nest over the breeding season (month vs. no. hatchlings, $\chi^2 = 17.9$, $df = 3, 153$, $p < 0.01$). Hatching success (total no. hatchlings/total no.

eggs in nests at hatching) was 89.8% ± 0.013 (675 hatchlings from 752 eggs in 209 nests). Hatching success varied over the years, though this was not quite significant ($\chi^2 = 11.3$, df = 6, p = 0.08). There was no significant difference between hatching success at Kowhai Bush and in Ireland (Table 2.2; Wilcoxon rank sum: W = 11175, p = 0.71).

Mean number of fledglings per nest was 2.62 ± 0.085 (n = 125 successful nests). There was a significant difference between months (month vs. no. fledglings $\chi^2 = 28.1$, df = 3, 153, p < 0.01). Of 103 successful nests, where clutch size, hatching success and number of fledglings was known, 30 (29.1%) experienced brood reduction and 45 nestlings died before fledging. Although some incidences were the result of nestlings falling out of nests that had tilted (the proportion of deaths caused by poor nest construction was probably slightly higher amongst unsuccessful nests that experienced brood reduction before failure), more than 93% of deaths in successful nests appeared to be the result of starvation. Breeding success was significantly lower at Kowhai Bush than in Britain (Table 2.2; t = -12.11, df = 337, p < 0.01). Using the formula for calculating reproductive output per attempt (ROA, Paradis *et al.* 2000) I calculated a value of 0.78 for song thrushes in New Zealand which was considerably lower than that reported for the UK (Table 2.2).

Daily nest survival rates were similar during the egg (laying + incubation) and nestling stages at Kowhai Bush (Table 2.3). The overall probability of a song thrush nest surviving at Kowhai Bush was 24.0% (based on a mean egg stage duration of 18.3 days and a nestling stage of 12.7 days). This is higher than that calculated from daily survival rates in two Irish populations (19.4%, Kelleher & O'Halloran 2006), where nest survival was lower than at Kowhai Bush during the egg stage, but slightly higher for the nestling stage. However, daily survival rates of thrush nests in England were higher than the rates at Kowhai Bush for both nest stages (Table 2.3).

There was a significant relationship between nest predation and month among thrush nests at Kowhai Bush ($\chi^2 = 5.32$, df = 357, p < 0.05), with more nests being depredated later in the season. Significantly more nests were also abandoned later in the season ($\chi^2 = 4.80$, df = 317, p < 0.05), so early nesting attempts appear to be more successful. Nest failure was caused by predation (58.8% of failures), abandonment (37.3%) and severe weather/poor nest construction resulting in nests tipping over or falling out of the tree (3.9%); these values are similar to those found in Ireland (Table 2.4).

Incubation period could be calculated accurately (to within 1 day) for 54 nests. Mean incubation period was 14.7 days ± 0.195, which is significantly longer than the incubation period in Britain (13.4 days, Table 2.2; $t = 6.86$, $df = 53$, $p < 0.01$). There was no effect of clutch size on length of incubation period ($F = 0.67$, $df = 3, 50$, $p = 0.57$). Mean nestling period was 12.7 days ± 0.130 ($n = 81$), which is significantly shorter than the nestling period in Britain (13.2 days; $t = -3.53$, $df = 80$, $p < 0.01$), and there was also no effect of clutch size ($F = 2.00$, $df = 2, 76$, $p = 0.14$).

Nest size was measured for 160 nests over the 2006-08 breeding seasons. Inner volume (204.7 cm^3 ± 3.8) was less variable than outer volume (1437.9 cm^3 ± 35.1). There was no relationship between inner volume and either clutch size ($F = 1.47$, $df = 3, 75$, $p = 0.22$) or nest height ($F = 2.32$, $df = 1, 158$, $p = 0.13$). Outer volume decreased significantly with nest height ($F = 15.4$, $df = 1, 158$, $p < 0.01$), but was not related to clutch size ($F = 1.14$, $df = 1, 142$, $p = 0.34$). There was a significant difference between mean outer volume in Kowhai Bush and that recorded in the literature for a Polish population (Table 2.2; $t = -16.4$, $df = 159$, $p < 0.01$), but no difference in inner volume (197.3 cm^3; $t = 0.68$, $df = 159$, $p = 0.50$) or mean nest height (Table 2.2; $t = 0.521$, $df = 413$, $p = 0.60$). The ratio of inner:outer volume was significantly higher at Kowhai Bush (Table 2.2; $t = 15.0$, $df = 159$, $p < 0.01$); i.e., inner nest volume was larger relative to outer volume. Those nests with a larger inner volume relative to the outer volume were also significantly more successful, both in terms of the number of fledglings produced per nest ($F = 18.0$, $df = 1, 133$, $p < 0.01$), nest success ($\chi^2 = 8.1$, $df = 1, 148$, $p < 0.01$) and abandonment rates (nests with smaller inner relative to outer were abandoned more often, $\chi^2 = 7.03$, $df = 1, 154$, $p < 0.01$). Inner nest volume was also significantly related to both nest success ($\chi^2 = 24.1$, $df = 1, 148$, $p < 0.01$) and number of fledglings ($F = 25.5$, $df = 1,133$, $p < 0.01$).

2.5 Discussion

Several life-history traits appear to have changed in New Zealand song thrushes since their introduction from Britain, with significant changes observed in clutch size, egg size and shape, incubation and nestling period lengths, breeding success, and nest size (Table 2.2). The changes were predominantly 'negative', with song thrushes in New Zealand building smaller nests, laying smaller clutches and smaller eggs, having shorter nestling periods and producing fewer fledglings, which suggests a decrease in the overall investment per nesting attempt. One trait which appears to have

increased compared with Britain is the incubation period. However, this may be the result of females reducing incubation attentiveness (percent time spent incubating), and is therefore another possible example of decreasing investment. Also, early nesting attempts appear to be more successful at Kowhai Bush, though this may not be true for British and Irish populations (Snow 1955b, Kelleher & O'Halloran 2006), or even other populations in New Zealand (Evans *et al.* 2005), suggesting that conditions at Kowhai Bush may rapidly become less ideal for breeding.

One reason for a bird to reduce its investment in any single reproductive bout is if the value of that bout has decreased. For example, higher failure rates, whether resulting from increased levels of predation or some other factor, may select for reduced clutch sizes (Skutch 1949, Slagsvold 1984). I found that breeding success (the proportion of eggs that were converted to fledglings) and ROA were both lower at Kowhai Bush than in Britain and Ireland (Cramp 1988, Paradis *et al.* 2000, Kelleher & O'Halloran 2006), which suggests that the fitness benefits of each clutch have indeed decreased relative to the source population. This is further supported by a study of thrush nests from different habitats near Hamilton (labelled in Fig. 3.1) that found even lower rates of success (<10%; Cassey *et al.* 2009). Kelleher & O'Halloran (2006) also found lower reproductive success in Ireland compared to Britain, and they proposed that Ireland's milder climate allowed for higher adult survival and consequently increased competition during the breeding season, which could also be the possible cause of lower reproductive success in New Zealand, as high rates of brood reduction (individual nestling mortality) suggest that many pairs struggle to provide enough food to their young. For successful nests where clutch size, brood size and fledgling success were known, 29.1% experienced brood reduction. In contrast, rates of brood reduction (or "partial failure") in Britain are low (Kelleher & O'Halloran 2006); for example, Lack (1949) reported 96% survival of nestlings from successful nests. If this higher rate of starvation indicates that thrushes are limited in the number of nestlings they can successfully raise in New Zealand, it may be that selection is acting specifically on reduced clutch size rather than to decrease overall investment in any one reproductive bout. However, increased adult survivorship could also 'devalue' individual bouts by enabling birds to initiate more bouts over their lifespan or by selecting for lower reproductive effort via tradeoffs between survival and reproduction (Stearns 1992). I was unable to get sufficient data on survival rates of adults at Kowhai Bush to assess

this possibility, but there is anecdotal evidence to suggest that birds are living longer in New Zealand (Evans *et al.* 2005).

Smaller nests probably require less effort to build, and in New Zealand's warmer climate, nests as large as those in Europe may not be necessary for their insulative properties (Lamprecht & Schmolz 2004, de Heij *et al.* 2006). Nevertheless, the positive relationship with nest success suggests that relatively larger nests may be beneficial at Kowhai Bush, though this may reflect female quality rather than any property of the nest itself (Soler *et al.* 2001, Tomas *et al.* 2006, Mainwaring *et al.* 2008), particularly as there was a significant relationship between nest size and nest desertion. For example, Broggi & Senar (2009) found that great tit (*Parus major*) females in good condition and females paired to males in good condition (based on breast plumage colouration) built larger nests, which may signal the female's intention to invest more than the minimum required level, or encourage the male to invest more. Reduced clutch size at Kowhai Bush could also have rendered larger nests unnecessary, as nest size can be related to clutch size and overcrowding in the nest may limit the reproductive success of larger clutches (Slagsvold 1982). Lower food availability may also select for decreased nest size, because nest building is costly (Mainwaring & Hartley 2009).

Reduced conspicuousness of smaller nests to predators could potentially offset the increased exposure to predators resulting from longer incubation periods. However, many studies have found no evidence that nest size affects the likelihood of predation (e.g., Palomino *et al.* 1998, Weidinger 2004, Suarez *et al.* 2005), particularly for predators who use olfactory cues to find nests (Colombelli-Negrel & Kleindorfer 2009), as is likely the case for most mammalian predators at Kowhai Bush. A reduced nestling period may offset some of the extra incubation time, but these two stages still take an extra half day to complete in New Zealand. Since selection is likely acting to reduce the length of the nesting period (especially as later broods are less successful), this suggests some limitation on incubation ability at Kowhai Bush. Females may be adaptively investing less energy into incubation, or the decrease in clutch size may affect the clutches' cooling properties (Reid *et al.* 2000), thus requiring more energy to achieve the same degree of incubation. Additional effort may not be adaptive, despite the increase in predation risk of longer incubation periods, though smaller nests may assist with heat retention and potentially negate the effect of fewer eggs (Slagsvold 1989) and lower levels of incubation may reduce nest conspicuousness to predators, if parental activity affects

predation and is correlated with incubation effort (Conway & Martin 2000). A comparison of incubation attentiveness (percent time spent incubating) and number of visits to the nest between British and New Zealand birds would clarify whether females are incubating for different amounts of time, while temperature probes could determine if females are providing the same degree of incubation during on-bouts. Alternatively, food limitation may require females to forage for longer to attain the same nutritional gains, which may reduce the time they can spend incubating (e.g., Chalfoun & Martin 2007). The decrease in clutch size (half an egg, on average) also reduces the length of the laying period (one day fewer per egg not laid) and thus the length of each reproductive bout, so it is possible that selection for smaller clutches is also related to tradeoffs between the length of each nesting stage and the duration of the most favourable breeding conditions.

While the reason for several changes in life-history traits may be lower reproductive output, it is unclear why breeding success in New Zealand is lower than in Britain. Predation rates were similar, and possibly lower at Kowhai Bush, while the proportion of abandoned nests was higher. As a result, overall numbers of successful nests are similar between New Zealand and Britain, so it appears to be the relative output of successful nests that differs. Smaller clutches and a greater occurrence of brood reduction in New Zealand may be the result of continuing selection for smaller clutches, based on food limitation during the nestling stage (Lack 1947), but an increase in adult lifespan could also enable individuals to make more nesting attempts and thus affect the tradeoff between current and future reproduction (Godfray *et al.* 1991, Stearns 1992). Nest desertion rates were higher in New Zealand, which suggests that there are differences in parental behaviour between New Zealand and Britain, perhaps as a result of lower value of clutches in New Zealand. Experimental tests to assess the ability of parents to raise more offspring in any one reproductive bout could determine whether the New Zealand environment restricts the number of nestlings they can fledge (i.e., the decrease in clutch size is directly adaptive). Alternatively, data on adult survivorship and the effects of enlarged broods on subsequent parental fitness would provide information regarding the likelihood of higher survival probabilities in New Zealand selecting for an overall reduction in investment per nesting attempt, because more attempts are possible in New Zealand.

Further studies on the life-history traits of other song thrush populations in New Zealand and Britain, both observational and experimental, would enable more detailed comparisons and show the

widespread nature of changes in life-history traits. Although song thrush numbers have been declining in Britain in recent history (Peach *et al.* 2004, Robinson *et al.* 2004), they have become one of the commonest land birds in New Zealand (Robertson *et al.* 2007). The reason for this difference is not clear, but their abundance in New Zealand, despite lower breeding success, suggests that post-fledging survival is indeed the main factor affecting British populations, as proposed by Robinson *et al.* (2004). If climate change results in the British climate becoming warmer and drier (i.e., more similar to that of New Zealand), this may further affect song thrush populations through decreases in reproductive success, which could select for reduced investment in reproduction. The life history changes observed among thrushes in New Zealand may provide a glimpse into how thrushes will adapt to environmental warming in their native range.

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Table 2.1. Year-by-year break-down of sample sizes for the life-history traits measured in song thrushes nesting at Kowhai Bush, Kaikoura.

Sample sizes per year	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**Total**
Nests followed	47	70	45	40	52	67	94	415
Clutches measured (egg size)	0	5	8	8	36	44	53	154
Broods measured	–	–	–	–	21	19	19	59
Nests measured	–	–	4	2	37	50	67	160
Nests with known outcome	38	59	30	37	44	62	89	359

Table 2.2. Life-history values (mean ± SE) for song thrush populations in an introduced population at Kowhai Bush, New Zealand, and native (British/European) populations, as reported in the literature. Sample sizes for means from Kowhai Bush and percent differences between Kowhai Bush and the native range are given in parentheses. **Denotes significant difference at $p < 0.01$.

Trait	Kowhai Bush (KB)	United Kingdom (UK)	Other European populations	Difference (KB–UK)
Clutch size	3.56 ± 0 .032 (367)	4.09 eggs [a(1)] 4.10 ± 0.67 [b]	4.24-4.88 [h]	-0.54 eggs (-13.2%)**
Egg size	5.60 cm^3 ± 0.04 (154)	6.02 cm^3 ± 0.092 [c]	5.64 cm^3 [i]	-0.42 cm^3 (-7.0%)**
Egg shape	1.325 ± 0.005 (154)	1.297 ± 0.011 [c]	1.322 [i]	+0.028 (+2.2%)**
Hatching success	89.8% ± 0.013 (209)	91-96% [a(2)]	89.6% [d]	-1 to -6%
Incubation period	14.7 days ± 0.20 (54)	13.4 days [e] 14.18 ± 1.23 [b]	–	+1.3 days (+8.8%)**
Nestling period	12.7 days ± 0.13 (81)	13.2 days [e] 14.01 ± 1.15 [b]	–	-0.5 days (-3.8%)**
Breeding success	23.5% ± 2.1 (338)	55% [e]	–	-31.5%**
Nest desertion (% of nests)	24.2% (359)	15% [d]	–	+9.2%
Brood reduction	14% (103)	4% [f]	–	+10%
Reproductive output per attempt (ROA)	0.78	1.63 ± 0.366 [g]	1.13 [d]	-52.1%
Nest volume (outer)	1437.9 cm^3 ± 35.1 (160)	–	2012.8 cm^3 [j]	-574.9 cm^3 (-28.6%)**
Nest size ratio (inner:outer)	0.151 ± 0.004	–	0.098 [j]	+0.053 (+35.1%)**
Nest height	2.5 m ± 0.06 (160)	–	2.5 m [j]	+ 0 m

References (data source): [a(1)]Snow (1955a) (UK), [a(2)]Snow (1955b) (UK), [b]British Trust for Ornithology (2005) (UK); [c]Congdon & Briskie (2010) (UK); [d]Kelleher & O'Halloran (2006) (Ireland); [e]Silva (1949) (UK); [f]Lack (1949) (UK); [g]Paradis *et al.* (2000) (UK, variance measure is standard deviation); [h]Järvinen (1986) (Finland), Weidinger (2001) (Czech Republic); [i]Schönwetter (1979) (central and eastern Europe); [j]Bocheński (1968), cited in Cramp (1988) (Poland).

Table 2.3. Daily nest survival rates (± SE) for New Zealand and British populations during the egg (laying + incubation) and nestling stages, with reproductive output per attempt (ROA; number of fledglings per nest). Nest survival was similar for both the egg and nestling stages in New Zealand, but was highest during the nestling stage in Britain. Song thrushes in New Zealand have similar rates of daily nest survival, yet ROA is much lower.

Country	Daily nest survival rate		Reproductive output per attempt
	Egg stage	Nestling stage	
New Zealand	0.9563 ± 0.0002	0.9530 ± 0.0003	0.78
Britain	0.962	0.976	1.63
Ireland	0.9362 ± 0.0126	0.9609 ± 0.0096	1.13

Data sources: New Zealand: this study; Britain: Paradis *et al.* (2000), means calculated from daily failure rates; Ireland: Kelleher & O'Halloran (2006), type of error term not specified.

Table 2.4. Causes of nest failure for the egg (laying + incubation) and nestling stages in New Zealand and Ireland (Kelleher & O'Halloran 2006), modelled on Table 2 of Kelleher & O'Halloran (2006).

Cause of failure		Number of nests		Percentage per nest stage		Percentage per failure	
	Stage	**NZ**	**Ireland**	**NZ**	**Ireland**	**NZ**	**Ireland**
Desertion	Egg	65	11	27.9	24.4	36.5	33
	Nestling	20	4	8.6	8.9		
Predation	Egg	67	19	28.8	42.2	59.2	67
	Nestling	71	11	30.5	24.4		
Other	Egg	6	–	2.6	–	4.3	–
	Nestling	4	–	1.7	–		
Total		**233**	**45**	**100**	**100**	**100**	**100**

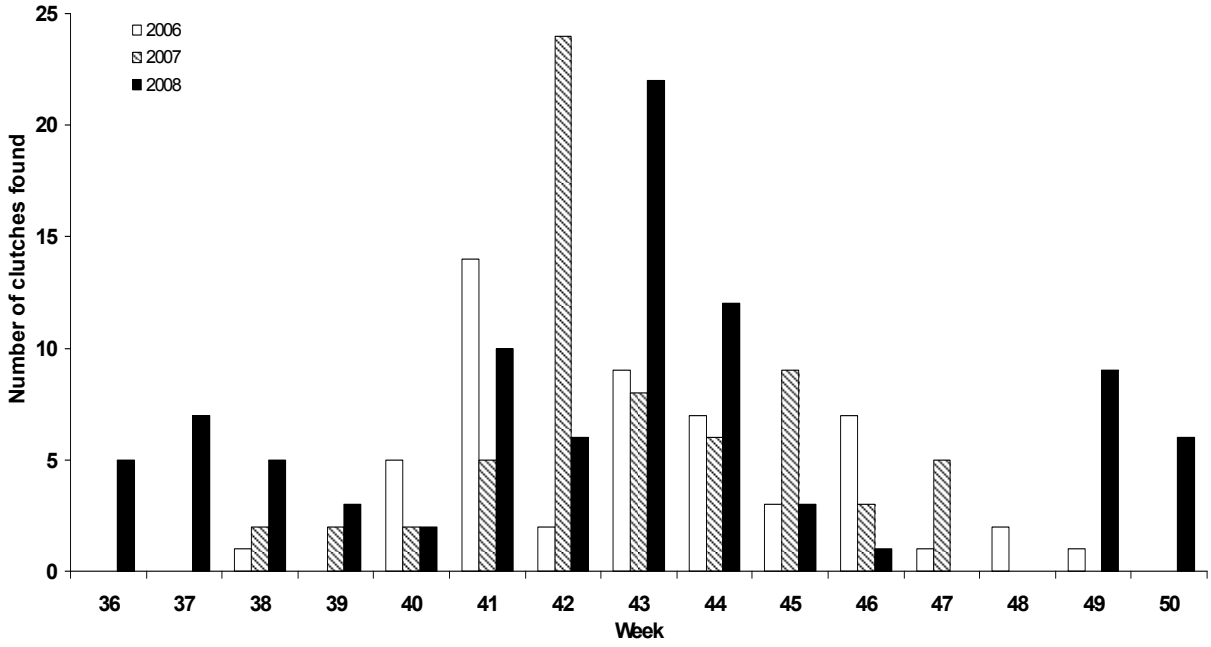

Figure 2.1. Number of clutches initiated per week at Kowhai Bush over 2006-2008 (based on date of first egg). Each breeding attempt takes approximately 4.5 weeks from the laying of the first egg to fledging; because the female usually begins building the next nest while the male is still feeding fledglings, the gap between clutches is only 1-2 weeks. In 2006, there was one main peak in the second week of October (week 41), then a decline, until another smaller peak mid-November (week 46). In 2007, the first peak was a week later (week 42), then the number of new nests dropped but remained relatively constant with a smaller peak in week 45. In 2008, breeding began earlier, with the first peak in the second week of September (week 37), then numbers of new nests peaked again at weeks 41 and 43 and a final peak was observed in early December (week 49).

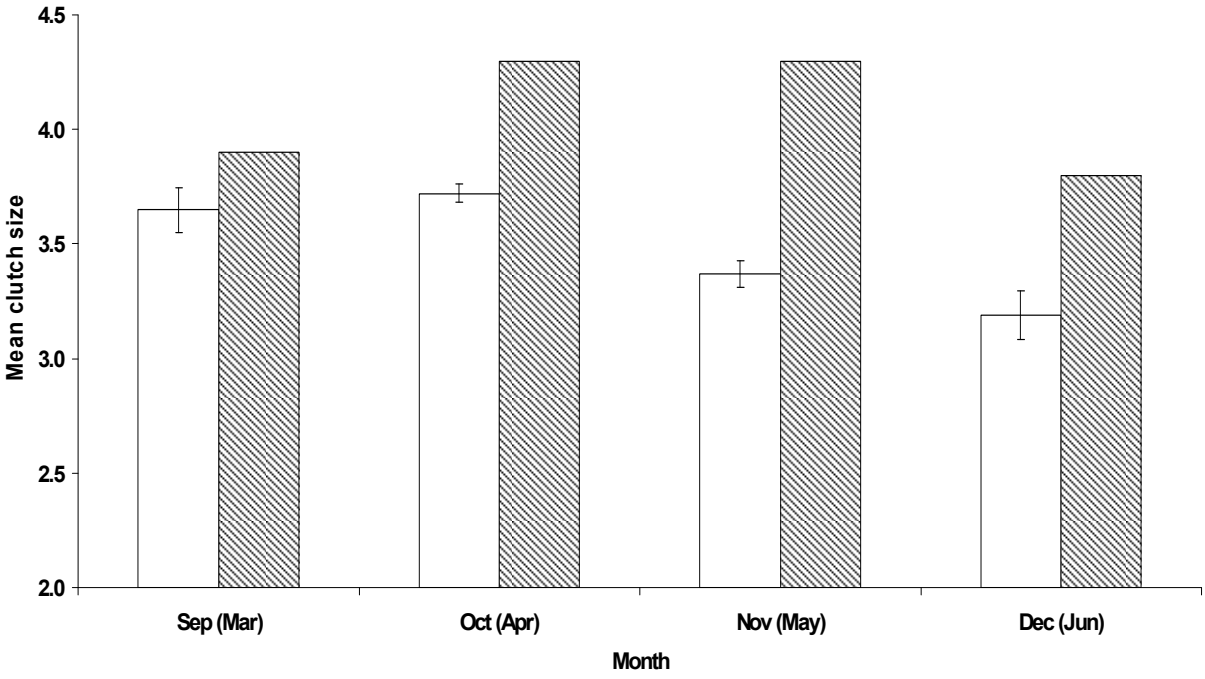

Figure 2.2. Mean clutch size between months for Kowhai Bush (unshaded bars ± SE) and a British population (shaded bars; means taken from Cramp 1988).

=== Chapter 3 ===

Geographic variation in clutch size of song thrushes (*Turdus philomelos*) in New Zealand

3.1 Abstract

Geographic variation in clutch size has been suggested to result from differences in latitude and/or climatic differences between regions. To examine variation in clutch size among introduced populations of song thrushes (*Turdus philomelos*), and whether it varies with latitude or climate, I compiled information on clutch size and other measures of reproductive success from the nest record database of the Ornithological Society of New Zealand and with data from the literature on native European populations. Clutch size was significantly smaller in New Zealand than in the source population of thrushes in Britain. This decrease likely occurred shortly after introduction, as clutch size of thrushes in New Zealand has not changed since at least the 1940s. Clutch size of song thrushes increased with latitude within Europe, and the mean clutch size of thrushes in New Zealand was the same as that expected for their lower latitude. This suggests the decrease in clutch size may be a function of environmental differences associated with latitude, although there was no relationship between clutch size and latitude within New Zealand, as would be expected if latitude alone was driving changes in clutch size. However, clutch size increased significantly with increasing rainfall and was significantly higher in New Zealand cities with higher annual rainfall than Britain. Fledging success was also significantly higher in these cities compared with cities with similar or lower rainfall. Low rainfall may limit reproductive success by reducing access to soil invertebrates during the nestling stage, and this may have favoured a reduction in clutch size in the drier regions of New Zealand. Song thrushes have only been established in New Zealand since the 1870s, yet it is apparent that some geographic variation in clutch size has already developed. This suggests song thrushes may be adapting to local conditions, such as lower rainfall than that experienced in the native range.

3.2 Introduction

Latitudinal and geographic differences in clutch size pose intriguing questions for evolutionary biology, as the underlying causes for such patterns are often not clear. Changes in clutch size with latitude have been found for many bird species (Skutch 1949, Lack 1968, McNamara *et al.* 2008); for example, species in the tropics typically lay only 1-2 eggs per clutch, while closely related species in temperate latitudes produce clutches of 3-6 eggs (Martin 1996, Jetz *et al.* 2008). A number of hypotheses have been proposed to explain both latitudinal and geographic variation in avian clutch size, but no single factor has been found to consistently drive observed patterns in all regions of the world. Lack (1947) first suggested that latitudinal patterns of clutch size could be explained by differences in the ability of birds to provision young. He proposed that food limitation selects for a modal clutch size that is equal to the number of nestlings which parents can raise. As the hours of daylight are fewer in low latitude environments (e.g., 12 hours of daylight at the Equator vs. 18 hours at 50°N), this may limit the time available per day to provision nestlings and thus select for lower clutch sizes.

While some studies support Lack's (1947) hypothesis (e.g., Sanz 1999, Dunn *et al.* 2000, Sanz *et al.* 2000), food availability may not be the most important, or the only, factor driving geographic variation in clutch size for all species. For example, nest predation has also been shown to influence clutch size (Skutch 1949, Olsen *et al.* 2008), as have differences in offspring and adult survivorship (Stearns 1992, de Heij *et al.* 2006). The energetic costs of breeding (i.e., egg production, incubation) may also influence the evolution of clutch size (Monaghan & Nager 1997, Martin 2002, Pérez *et al.* 2008), although few supplemental feeding experiments have found evidence for consistent positive effects on clutch size (e.g., Martin 1987, Sandercock *et al.* 2005, Bourgault *et al.* 2009). Climatic variables, such as temperature and rainfall, may also affect clutch size by influencing food availability (i.e., as above), nestling condition, or the cost of parental care in ways that could either enhance or reduce the effects of latitude. For example, Pérez *et al.* (2008) found that heating the nest box during incubation increased female feeding rates and nestling mass in tree swallows (*Tachycineta bicolor*). Hence, warmer temperatures at lower latitudes may decrease the costs of incubation and this could either alleviate selection against larger clutches that are more costly to incubate (e.g., Hanssen *et al.*

2003, de Heij *et al.* 2006) or lose heat less rapidly (Reid *et al.* 2000). Conversely, increased temperature could also favour smaller clutches via its effect on egg viability (e.g., Cooper *et al.* 2005).

Clutch size has decreased in several passerine species, including the song thrush (*Turdus philomelos*), introduced to New Zealand from Britain in the mid-19th century (Evans *et al.* 2005), and this may be the result of latitudinal differences between the two countries. As Britain (~50-60°) lies further from the Equator than New Zealand (~34-48°), the days are shorter in New Zealand during the breeding season and this may limit foraging time. Although New Zealand's warmer climate may offset some of the costs British birds pay when incubating eggs and brooding young under cooler temperatures, song thrushes appear to be food limited during the nestling stage (Chapter 2), so factors affecting food availability, such as daylength, may be more important for this species and the difference in latitude could therefore drive selection for smaller clutches in New Zealand. Rainfall patterns also differ between Britain and New Zealand, so populations in some parts of New Zealand experience hotter and drier summers (e.g., the Canterbury region) than in the native range, while other populations inhabit areas that are wetter and warmer than in the native range (e.g., the West Coast and Northland regions). As earthworms are the song thrush's primary prey (Gruar *et al.* 2003), rainfall may provide a useful proxy for food availability in this species. Thus, clutch size may not have decreased in wetter regions, where food supply may be equivalent or greater than British levels. Conversely, decreases in drier regions may be greater than expected from the change in latitude alone, if the combination of low rainfall and low latitude increases the negative effect on reproductive success and clutch size.

Throughout the song thrush's native range of Britain and Europe, 4- and 5-egg clutches appear to be the most common, though there is evidence for latitudinal differences in clutch size. For example, Silva (1949) compared British and Dutch data and found lower clutch sizes in the lower latitude British sites. Similarly, Kelleher & O'Halloran (2006) compared two Irish populations and found that clutch size was lower in the site at lower latitude (although latitude and altitude may have been correlated in their study). New Zealand sits at the equivalent latitude of Spain and France, thus it is possible that the decrease in clutch size among introduced birds is due primarily to changes in latitude between their native and introduced ranges. In this chapter, I used data extracted from the Ornithological Society of New Zealand's (OSNZ) national database to determine whether the clutch

size of song thrushes varies with latitude and climatic region within New Zealand, and whether there is any evidence for changes in clutch size over time. I also tested whether the change in clutch size between New Zealand and the source population is due to differences in relative latitude (i.e., distance from the Equator). Finally, I compared clutch size and the number of hatchlings/fledglings in 14 New Zealand cities with mean annual rainfall, temperature and hours of sunshine to determine whether clutch size and reproductive success might be correlated with differences in climate within New Zealand. I expected that reproductive success would decrease with lower rainfall; birds in regions of lower rainfall (especially relative to that in the native range) are likely to have reduced access to earthworms, their primary prey (Gruar *et al.* 2003), which may have led to adaptive declines in clutch size.

3.3 Methods

Nest records from the OSNZ national database were used to estimate clutch size and breeding success of song thrushes across New Zealand. The records in the database have been collected by volunteers and researchers from throughout New Zealand for many bird species and despite its limitations (e.g., more mistakes are likely when there are multiple observers and transcribers), it is the largest nationwide collection of breeding records. For song thrushes, the data include information spanning several decades (1927-2001), with 150-300 records from each decade between 1960 and 1990. Of the 1,479 records for song thrushes available in the nest record scheme, 129 records were excluded from further analyses, predominantly because visits were too infrequent to confirm nest stage and/or the nest was empty on the second visit after the contents were first determined. Nine nests from offshore islands were also removed, along with other records containing obvious errors. For example, records were excluded if more than one egg appeared in the nest within a 24-hour period (suggesting an error in observations or recording) or if the notes attached to that record made no sense with respect to the contents of the nest in the spreadsheet (i.e., incorrect data entry).

To analyse variation in clutch size with geographic differences in climate variables, nest records were grouped by location, primarily around the largest towns and cities, as this is where most nest records originated. This resulted in a dataset of 1,073 nests from 14 city regions within New Zealand (Table 3.1). Each town or city was defined as an area within 1° of latitude/longitude of the city centre.

Locations with < 20 nest records were excluded. Centres with > 20 nests were spread over most of the country, providing a reasonable distribution of nests across the different climatic regions of New Zealand (Fig. 3.1), although the South Island's west coast is poorly represented. Mean annual rainfall (mm), temperature (°C) and sunshine hours for each city were gathered from the Cliflo climate database (NIWA 2010), based on weather data from 1971-2000 (the period containing most nest records).

Clutches were assumed to be complete when the number of eggs in the nest remained constant for two consecutive visits, or if there were nestlings present on the next visit, where the visits were less than 9 days apart (i.e., incubation must have been underway on the previous visit, so the clutch was complete). If a nest was found with newly-hatched nestlings (< 1 day) or contained eggs and nestlings < 1 day old, clutch size was defined as the number of nestlings (or eggs plus nestlings). Nests were counted as successful if at least one nestling fledged, while fledging success was defined as the number of nestlings in a nest that fledged. Failed nests were divided into depredated nests (broken eggs, depredated nestlings in or below the nest, or nest found empty before first possible fledging date), abandoned nests (intact eggs remaining in nest for >15 days with no sign of parent, eggs being cold after incubation had commenced, an accumulation of debris, or dead nestlings) and other (nests blown down or poor construction/site choice resulting in tilting). Some nests for which nest success was unknown contained nestlings that were ready to fledge (from 10 days old) and therefore were counted as successful. Where information from visits was insufficient to estimate nestling age to within 1-2 days, I took into account the observer's notes. For nests found with eggs (i.e., during laying or incubation), I also back-calculated hatching dates assuming that the incubation period was 14 days from the day the last egg was laid until the last egg hatches. Eggs were assumed to have been laid on the date they appeared in the nest, unless the visit was noted as occurring prior to 11:00 h (NZST), as song thrushes lay at midday, in which case the egg was counted as having been laid the previous day. Human activities (e.g., children removing a nest) were counted as predation, not abandonment, even if the nest and its contents were replaced. Brood reduction (pre-fledging nestling mortality) was measured as the difference between the number of fledglings and the number of hatchlings (i.e., unhatched eggs and failed nests were not included). All means are given ± standard error (SE).

Song thrushes in the north of New Zealand likely begin breeding earlier than those in the South Island, and the nest records appear to support this. Month of first egg was significantly earlier at lower

latitudes (One-way ANOVA: $F = 96.7$, $df = 1, 1348$, $p < 0.01$). Because I could not determine the exact length of the breeding season in each region, I assumed that the nest records represent a random sample of nests from throughout the breeding season in each region and thus that mean values incorporate changes over the breeding season.

Statistical tests were carried out in R 2.4.0 (R Development Core Team 2006). I used generalised linear models (GLMs, Crawley 2005) to test whether clutch size varies with time (decade of nesting attempt), latitude, climate (rainfall, temperature, sunshine hours; all log-transformed) or geographic location within New Zealand. Means from the literature were also used to compare clutch sizes of populations in various countries across ~35° of latitude using least-squares regression. There was a significant quadratic relationship with timing through the season (month of first egg: $F = 13.97$, $df = 1, 1008$, $p < 0.01$; month^2: $F = 24.66$, $df = 1, 1007$, $p < 0.01$); clutch size peaked in September and October and then declined over November and December. I therefore included month and month^2 in the models to control for seasonal effects. There was no significant interaction between decade and month for clutch size ($F = 0.79$, $df = 7, 993$, $p = 0.60$). To compare clutch sizes in New Zealand with those in Britain, I used two-sample t-tests on the clutch size data from each city region against a sample of clutch sizes from a British population (Snow 1955a). To test for differences in reproductive success (number of eggs hatched and number of nestlings fledged, including failed nests) between city regions, climate variables, and clutch sizes, I used GLMs but specified a quasi-Poisson distribution (as these variables were overdispersed). To compare differences in brood reduction with climate, I used a GLM with a Poisson distribution. Analyses including climate variables (which were log-transformed to meet the assumptions of GLMs) were nested within city, as nests in each city were assumed to experience the same average climate, and thus were not independent. Rainfall in Punakaiki was considerably higher than in the other city regions, but analyses excluding this region produced similar results, so only the results including Punakaki are presented here.

3.4 Results

Mean clutch size of song thrushes over their entire range in New Zealand was 3.81 eggs ± 0.019 ($n = 1010$). Differences in mean clutch size between countries and populations were significantly related to latitudinal differences (Fig. 3.2; $F = 22.8$, $df = 1, 13$, $p < 0.01$). Clutch size increased with increasing

latitude, with the regression line explaining 63.7% of variation in mean clutch size. From the regression equation, mean clutch size for song thrushes in New Zealand was predicted to range from 3.6 to 4.1 eggs per clutch (Fig. 3.2), which was similar to that observed in the 14 city regions (Fig. 3.3). However, there was no effect of latitude on mean clutch size within New Zealand (Fig. 3.3; $F = 2.69$, $df = 1, 1006$, $p = 0.10$). There was also no significant change in clutch size over time (measured in decades; $F = 1.28$, $df = 1, 1008$, $p = 0.26$), suggesting that the clutch size of song thrushes in New Zealand changed rapidly after their introduction and has been relatively stable since then.

After controlling for seasonal variation (i.e., month of first egg), clutch size of song thrushes was significantly different between the 14 city regions of New Zealand (Fig. 3.3; $F = 2.58$, $df = 13, 779$, $p < 0.01$). Mean clutch size varied from 3.55 to 4.12 eggs between cities (Fig. 3.1). The highest mean values (4.00 and 4.12) came from Punakaiki (west coast, South Island) and Opotiki (upper north-east coast, North Island) respectively. The lowest mean clutch size was from Dunedin (lower east coast, South Island). The mean clutch size of song thrushes in Britain, 4.09 eggs/clutch (Cramp 1988), was significantly different from the mean clutch size for nine of the city regions ($t = -7.7$ to -2.5, $df = 19$ to 197, all $p < 0.01$), with decreases of 6-13% relative to the British mean. Mean clutch size in Hamilton, Opotiki, Nelson, Punakaiki and Ashburton was not significantly different from the British mean ($t = -1.7$ to 0.28, $df = 18$ to 69, $p = 0.1$ to 0.8). Clutch size was significantly related to rainfall after controlling for seasonal variation and differences in latitude, with higher clutch sizes in cities with higher rainfall (Fig. 3.4; $F = 5.25$, $df = 1, 789$, $p < 0.05$).

The mean number of eggs hatched did not vary significantly between cities (range = 1.7 to 2.8 eggs hatched), whether controlling for clutch size ($F = 1.27$, $df = 13, 603$, $p = 0.23$) or not ($F = 1.62$, $df = 13, 693$, $p = 0.07$). After controlling for differences in clutch size, fledgling success (1.0 to 2.1 fledglings per nest, Fig. 3.3) varied significantly between city regions ($F = 2.20$, $df = 13, 548$, $p < 0.01$). This was not a result of differences in nest success between cities, as the number of fledglings was still significant when nest success was included in the model ($F = 3.38$, $df = 13, 547$, $p < 0.01$). Differences in nest success between city regions were significant ($\chi^2 = 23.73$, $df = 13, 546$, $p < 0.05$) after controlling for clutch size (not significant; $\chi^2 = 1.88$, $df = 5, 559$, $p = 0.87$). Fewer fledglings were produced as hours of sunshine increased (Fig. 3.4; $F = 14.1$, $df = 1, 506$, $p < 0.05$; controlling for clutch size: $F = 10.62$, $df = 1, 464$, $p < 0.01$); if included in the model after sunshine, temperature was

almost significant (F = 3.00, df = 1, 505, p = 0.08), with a positive effect on fledgling success. Brood reduction increased with hours of sunshine, though the relationship was not quite significant (χ^2 = 3.16, df = 1, 215, p = 0.08).

Nest success decreased significantly with hours of sunshine (χ^2 = 4.37, df = 1, 663, p < 0.05), because nest desertion rates increased significantly with hours of sunshine (χ^2 = 7.23, df = 1, 663, p < 0.05). There was no relationship between nest predation and any climate variables (e.g., hours of sunshine: χ^2 = 0.06, df = 1, 663, p = 0.07), though the positive relationship with latitude was approaching significance (χ^2 = 3.21, df = 1, 906, p = 0.07).

3.5 Discussion

Clutch size of song thrushes was generally smaller throughout New Zealand than in their native British range. There were also significant differences in clutch size with rainfall in New Zealand, while fledgling success was significantly related to hours of sunshine, with smaller clutches in cities that had lower levels of rainfall and fewer fledglings produced per nest in cities with more sunshine hours. Much of the decrease in clutch size between the native and introduced ranges appears to be related to latitude on a global scale as the clutch size of song thrushes in New Zealand is in line with that expected for the species at this latitude. However, somewhat surprisingly, latitude was not significantly related to clutch size within New Zealand, and it seems that other aspects of the climate independent of latitude may be driving differences in clutch size within the introduced range. Clutch size decreased with rainfall, suggesting that there may be selection against larger clutch sizes in New Zealand and that it may be most intense in dry regions.

The significant linear relationship in clutch size between populations at different latitudes throughout the world (Fig. 3.2) suggests that latitude is related to decreased clutch size in New Zealand, though the exact factor responsible is not clear. Lack (1947) proposed that decreased daylength at lower latitudes limits the number of offspring that can be fed, thus favouring reduced brood sizes. As New Zealand lies over 10 degrees closer to the Equator than Britain, we might expect clutch size to be lower and this in fact was the case. However, contrary to expectation, there was no significant relationship between clutch size and latitude within the New Zealand range of the song thrush. If daylength and foraging effects, as described by Lack (1947), were responsible for the

decrease in clutch size between the introduced and native ranges, then the same process should also have led to latitudinal changes within New Zealand. It is possible that the latitudinal range in New Zealand is too narrow to lead to any detectable difference in clutch size, though this seems unlikely given that the range from Northland to Southland (~10°) is the same (in relative terms) as between Britain and New Zealand. Alternatively, Evans *et al.* (2009) found an effect of daylength but not latitude on clutch size in British birds, so latitude may provide an equally poor estimate of daylength in New Zealand (e.g., thicker and longer cloud cover may shorten the available daylength for foraging more in some regions than others). Direct comparisons between daylength and clutch size are therefore required to confirm whether daylength affects clutch size within New Zealand. Nevertheless, my results found no change in clutch size with latitude (a proxy for more than just daylength), and this suggests that other climatic or environmental variables are responsible for the decrease in clutch size among New Zealand thrushes.

Mean clutch size was significantly different from the British mean for 9/14 New Zealand cities, which suggests that clutch size has not decreased uniformly throughout New Zealand. The cities where clutch size has apparently not decreased tended to have higher rainfall than cities with smaller mean clutch sizes, which suggests that the decrease in clutch size between Britain and New Zealand, and regional differences within New Zealand, may be linked to changes in rainfall patterns between the different populations. The link between rainfall and food availability has not been systematically studied, but it is possible that decreased rainfall could limit food availability in the form of earthworms and snails, which are two of the major prey items in the diet of both adult and nestling thrushes (Gruar *et al.* 2003). If dry, sunny weather makes it more difficult to locate prey items (e.g., worms bury deeper in the soil and out of reach, Gerard 1967), perhaps song thrushes are unable to collect enough food for nestlings, leading to higher rates of brood reduction and/or lower nestling condition, which may have led to selection for lower clutch size in dry regions. There is some anecdotal evidence from a long-term study site in Kaikoura that clutch size is directly linked to rainfall in a proximate fashion; only two 5-egg clutches were found over 2002-2007, then in 2008, when winter rainfall was over four times higher than average, three 5-egg clutches were found in that breeding season (pers. obs.). On the other hand, fledging success and rates of brood reduction were related to hours of sunshine but not rainfall. However, these may not be related to rainfall if the lower clutch sizes in these areas are more

in line with the brood size that birds, on average, can successfully raise. Clearly, the relationships between rainfall, food availability and clutch size are worth exploring further.

Although clutch size is likely the product of a number of selective forces, there was little evidence for any of the other alternatives that have been proposed to affect clutch size and reproductive success. Limitations in nutrient availability (e.g., low levels of soil calcium may limit egg production, Patten 2007, or hatching success, Schlender *et al.* 2007) are unlikely to explain the patterns I found, as there was no difference in the number of hatchlings per nest between cities. High rates of nest predation have also been suggested to favour reduced clutch size (Skutch 1949, Slagsvold 1984), but I found no differences in nest predation between cities, the rate was similar to predation in the native range (e.g., 66.6% of nest failures, Kelleher & O'Halloran 2006), and there did not appear to be higher predation on larger clutches (Chapter 2), as would be expected if predation risk had driven changes in clutch size. Weatherhead (2005) found no relationship between climate and clutch size in red-winged blackbirds (*Agelaius phoeniceus*), but did find a link between temperature and the onset of laying, and the same was found for blue tits (*Parus caeruleus*) in Croatia (Dolenec 2007). Whatever the explanation for why clutch size has decreased in New Zealand, the change probably occurred relatively rapidly after their introduction, as I found no significant change in clutch size over the five decades that my dataset spans. The decrease in clutch size appears to have occurred within the first 100 years of the introduction of thrushes to New Zealand, and highlights the speed at which changes can occur in some life-history traits.

This study is the first nationwide survey of clutch size of song thrushes in New Zealand. From the data currently available, it appears that song thrush clutch size differs significantly between cities and increases with rainfall, while hours of sunshine negatively affect reproductive success. Further research into what effect rainfall and sunshine have on food availability, and thus reproductive success, is necessary to confirm rainfall as the main factor driving variation in clutch size. For example, a more detailed study of a population in an area of high rainfall that receives ~2000 hours of sunshine annually, including experiments to test the birds' ability to incubate more eggs and/or raise more chicks, would allow comparisons with the 'dry' population at Kaikoura (Chapters 2 and 4). Because >50% of clutches contain four eggs, larger sample sizes in various regions would increase the number of other clutch sizes to allow a better estimate of mean clutch size. An assessment of breeding

season length for the different regions of New Zealand would also be of use; the pattern and/or magnitude of seasonal change in clutch size may vary between regions and could reflect local rainfall patterns over the breeding season.

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Table 3.1. Climatic comparisons between 14 city regions within New Zealand (Fig. 3.1). Climate data were sourced from NIWA (2010), based on weather data from 1971-2000.

City region	No. nest records	Mean annual temperature (°C)	Mean annual rainfall (mm)	Mean annual sunshine hours
Auckland (1)	79	15.6	1092	2044.80
Hamilton (2)	53	13.5	1207.9	2001.30
Opotiki (3)	34	14.1	1316.2	2159.4
New Plymouth (4)	29	14	1706.4	2173.2
Napier/Hastings (5)	70	14	741	2197.80
Palmerston North (6)	108	13	895.5	1757.8
Levin (7)	186	13.1	1105.2	1807.6
Nelson (8)	33	12.5	941.7	2404.5
Punakaiki (9)	81	13.6	2618.7	–
Kaikoura (10)	83	12.4	823.4	2082.3
Christchurch (11)	214	12.2	652.7	2100.1
Ashburton (12)	27	11.7	700.5	1885.70
Timaru (13)	54	11.2	550.7	1884.8
Dunedin (14)	22	10.3	684.8	1624.00

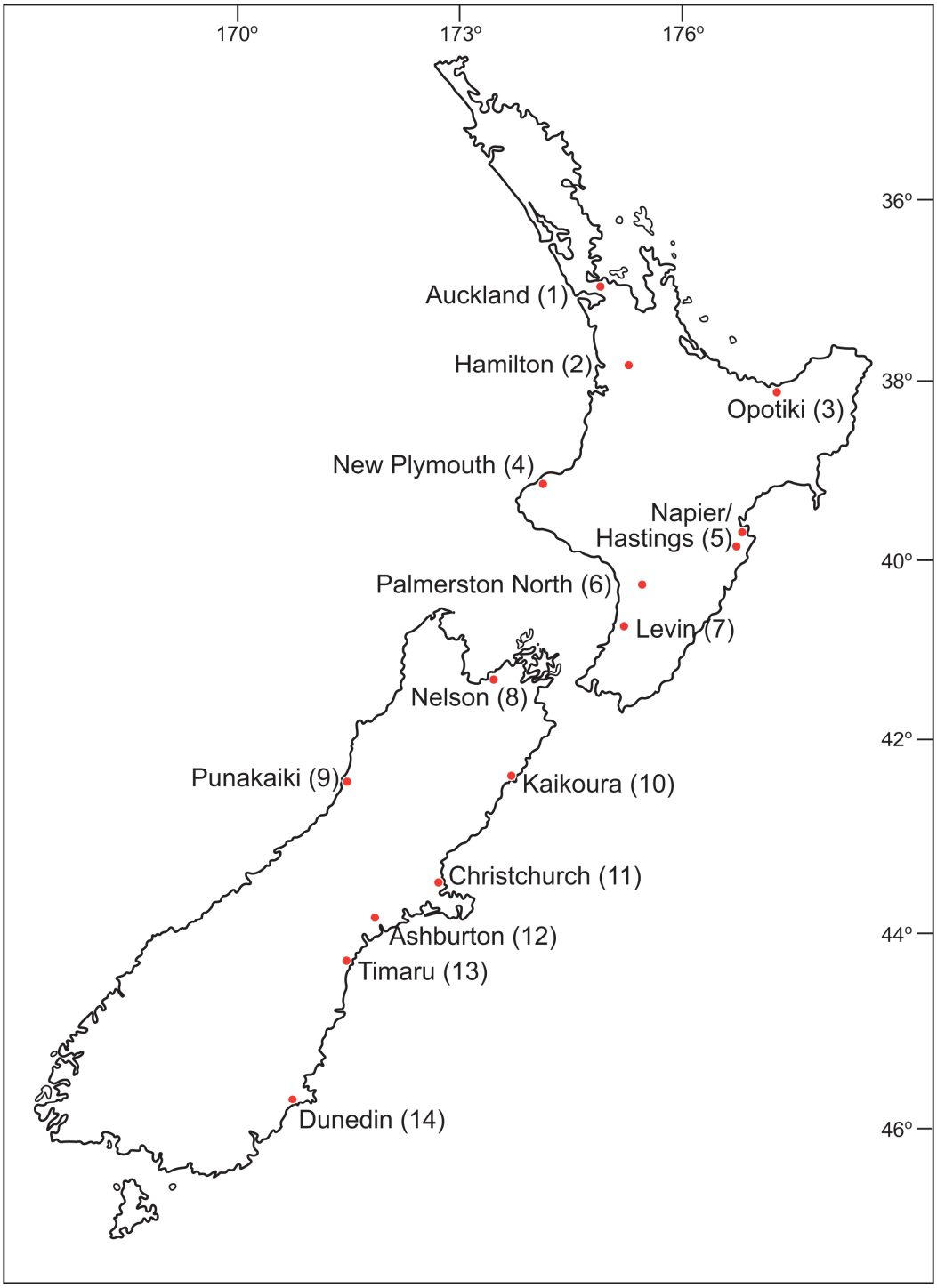


Figure 3.1. New Zealand map showing the 14 cities (numbered, as per points in Table 3.1 and Fig. 3.2) from which nest records were used for climate analyses.

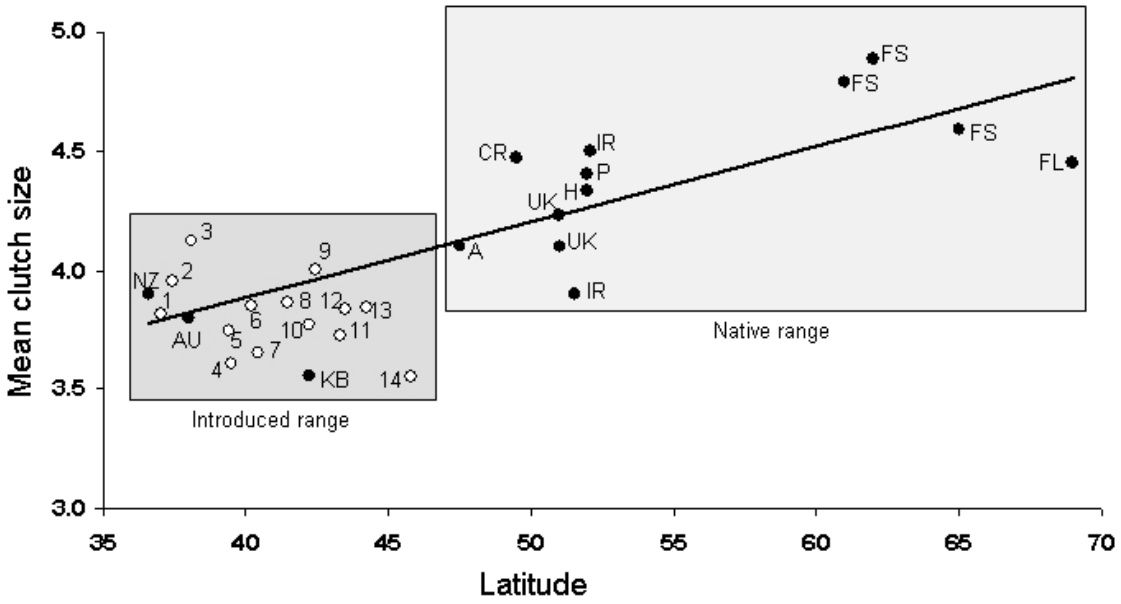
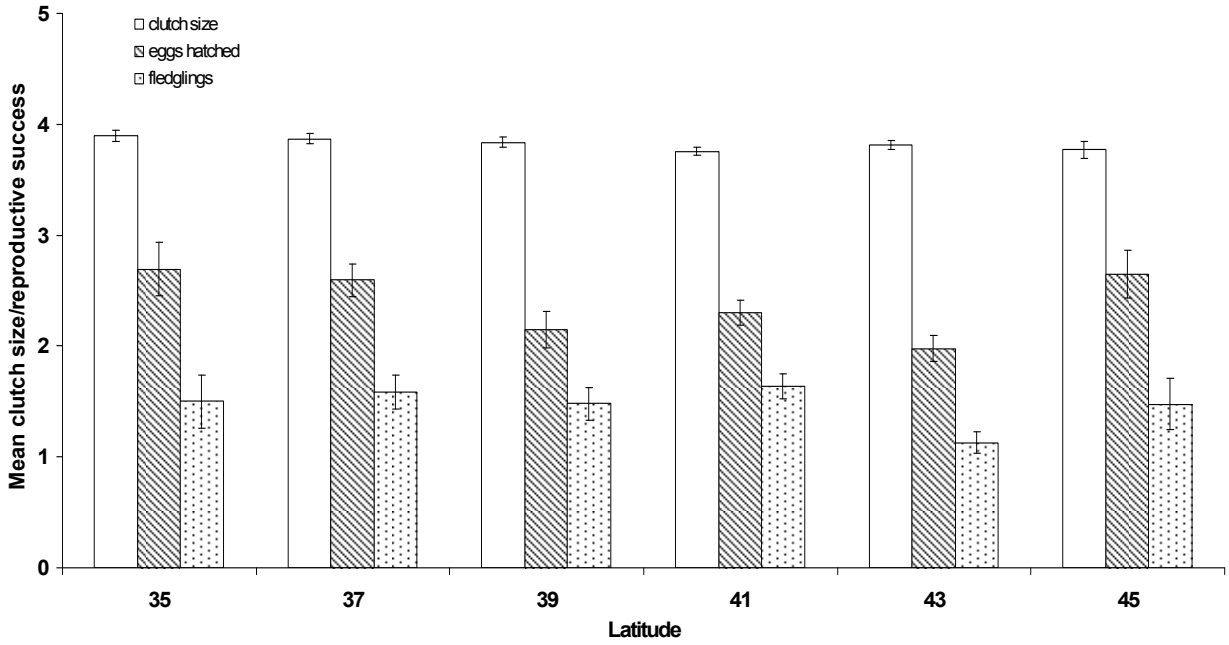


Figure 3.2. Mean clutch size of song thrushes in relation to latitude within New Zealand (white circles) and relative latitude from the Equator between countries (black circles).

Point Labels: 1-14: New Zealand cities (Fig. 3.1); A: Austria (47.5°); AU: Australia (38°); CR: Czech Republic (49.5°); FL: Finnish Lapland (69°); H: Holland (52°); IR: Ireland (51, 52°); KB: Kowhai Bush, New Zealand (42.2°); NZ: New Zealand (36.6°); P: Poland (52°); UK: southern Britain (51°); FS: Fennoscandia (61-65°).

Data sources: 1-14: this chapter; New Zealand: Mangere: Bull (1946), Kowhai Bush: Chapter 2; Australia: Melbourne: Higgins *et al.* (2006); Austria: Schnack (1991), cited in Kelleher & O'Halloran (2006); CR: Weidinger (2001); UK: Lack (1949) and Snow (1955a); Ireland: Kelleher & O'Halloran (2006); Holland: Silva (1949); Poland: Dycrz (1963) and Wesolowski & Czapulak (1986), both cited in Kelleher & O'Halloran (2006); Finnish Lapland/Fennoscandia: Järvinen (1986).

a)



b)

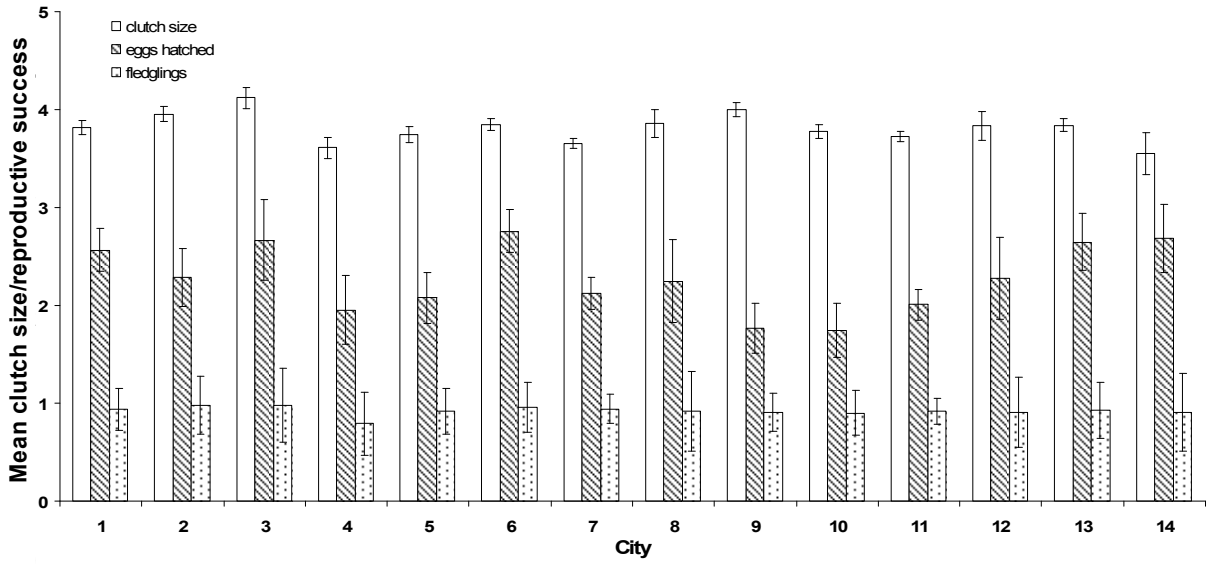
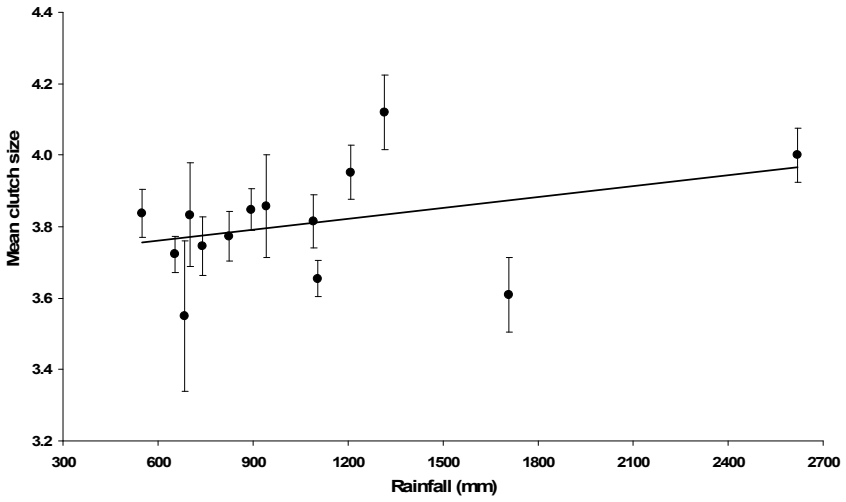


Figure 3.3. Differences in mean clutch size (± SE), number of eggs hatched, and number of nestlings fledged per nest for song thrushes in relation to: a) latitude across New Zealand, and b) 14 city regions of New Zealand (see Table 3.1 for city codes and sample sizes). Latitude was grouped into six categories, the midpoints of which were used to label the graph (the number of records between 46-48° was < 10, so the last category spans latitudes 44-48; sample sizes for the categories were 69, 171, 193, 417, 404, and 96 respectively).

a)



b)

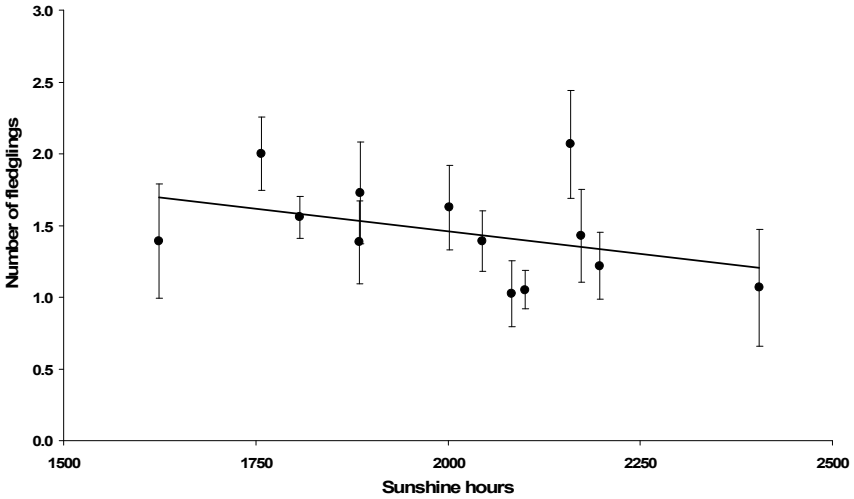


Figure 3.4. Relationships between life-history traits (mean ± SE) of song thrushes and climatic variables in 14 cities throughout New Zealand. Clutch size significantly increased with rainfall (a), and the number of nestlings fledged (fledging success) decreased with hours of sunshine (b). (Note, the data in this figure were analysed using logged values for rainfall and hours of sunshine, with controlling factors, such as timing within the season and clutch size, included in the models.)

=== Chapter 4 ===

Fitness effects of changes in egg morphology in an introduced population of song thrushes in New Zealand

4.1 Abstract

Changes in clutch size and egg size have been observed in several introduced bird species in New Zealand. Song thrushes (*Turdus philomelos*) in New Zealand lay both smaller clutches and smaller eggs than birds in the source (British) population, but it is uncertain whether the changes in egg size are sufficient to affect reproductive success. I measured variation in egg morphology of song thrushes in New Zealand and compared this to clutch size, laying date, mass loss, hatching success, parental behaviour, and the size and survival of the hatchling. Neither egg volume nor shape were directly related to clutch size. However, there was a significant interaction between egg size, clutch size and laying date; as the season progressed, clutch size decreased and eggs became larger and more pointed. Larger eggs produced significantly heavier hatchlings, but there was no effect of egg volume on hatching success. Loss of mass from eggs over the incubation period did not vary with either egg size or shape, but eggs that failed to hatch tended to be more pointed. Egg shape may be related to hatching failure directly, but female quality or condition may also affect hatching success via differences in incubation attentiveness, as females spent less time incubating clutches of more pointed eggs. Nests that experienced brood reduction (i.e., individual nestling mortality) also contained eggs that were significantly more pointed, further suggesting abnormal egg shape has a fitness cost. These results indicate that changes in egg shape among song thrushes in New Zealand are unlikely to be adaptive. Although it is less clear whether reduced egg size is also non-adaptive, a decrease in female body mass between thrushes in New Zealand and Britain suggests decreased egg size may simply be an allometric consequence of changes in body size.

4.2 Introduction

Song thrushes (*Turdus philomelos*) were introduced to New Zealand over 130 years ago and, in that time, both clutch size and egg size have decreased compared with the original populations in Britain (Evans *et al.* 2005, Congdon & Briskie 2010). Congdon & Briskie (2010) calculated that song thrush eggs in New Zealand had decreased by 5.5% in volume and become 2.2% more elongated (comparing mean length/width ratio in each population) since their introduction, but it is not known if these differences have any effect on hatching success or offspring fitness. Decreases in egg size may reflect changes in female body size in New Zealand (Congdon & Briskie 2010), increased resource constraints on females (e.g., calcium levels: Mänd & Tilgar 2003, Wilkin *et al.* 2009; and energy requirements of egg production: Magrath 1991, Krist *et al.* 2004), or be an adaptation to the novel environment in the introduced range. If the changes in egg morphology have a negative effect on hatching success and/or nestling survival, birds may pay these costs in terms of reduced fitness. Alternatively, selection favouring reduced investment in each reproductive bout, or reduced initial investment, could make laying slightly smaller eggs adaptive (Slagsvold 1984, Smith *et al.* 1995).

Variation in egg size has long intrigued researchers. Most studies have focused on defining patterns of egg size variation and the selective factors responsible. For example, egg size has been found to vary with laying date, ambient temperature (Lessells *et al.* 2002), female age, body size and condition (Hõrak 1994, Murphy 2004, Tryjanowski *et al.* 2004), territory quality, and clutch size (Figuerola & Green 2006). Variation in egg size within a clutch is also common, and consistent changes in egg size with laying order have been found in several species (e.g., Hõrak 1994, You *et al.* 2009). However, not all such variation is adaptive (Magrath 1991, Krist *et al.* 2004), and the strong allometric relationship between egg size and female body size (Deeming 2002) suggests that the ability of individual females to vary the size of their eggs may be constrained by the high heritability of egg size (Christians 2002). Until recently, the costs of egg production and incubation were considered minimal in comparison to the costs of raising nestlings (e.g., Lack 1947), but it is now accepted that these costs can be comparable (Thomson *et al.* 1998, Martin 2002, Pérez *et al.* 2008). Thus, selection on egg size could be affected by tradeoffs between offspring quality and the female's ability to invest in later stages of reproduction. The benefits of egg size are still debated, but smaller

eggs could be adaptive in some populations if the benefit to the offspring of being in a larger egg is not greater than the cost of producing a larger egg for the female.

While studies of egg morphology on offspring fitness do not show consistent results for all species, several authors have found significant fitness consequences, such as reduced hatching success in small eggs (e.g., Amundsen *et al.* 1996, Simmons 1997, Serrano *et al.* 2005) and abnormally-shaped eggs (Narushin & Romanov 2002). Similarly, larger eggs typically produce larger nestlings, which may be more likely to survive than lighter nestlings (Williams 1994), but the relationship between egg size and nestling size commonly disappears during the course of the nestling period (Smith *et al.* 1995, Amundsen *et al.* 1996, Christians 2002, Krist *et al.* 2004) and just as many studies have found no significant relationship between egg size and offspring survival (Williams 1994). This suggests that parents are generally able to compensate for the effects of egg size on offspring size/quality (i.e., the amount of food obtained post-hatching becomes the more important determinant of survival, e.g., Bolton 1991, Smith & Bruun 1998). However, birds may vary in their capacity to provide such compensation, perhaps as a result of experience or genetic quality, and poor-quality environments, or yearly variation in the availability of food and other resources, may also limit the ability of parents to provide sufficient food to their offspring (Christians 2002). Nevertheless, several studies have found a significant, lasting relationship between egg size and nestling survival (e.g., Styrsky *et al.* 2000, Silva *et al.* 2007, Wagner & Williams 2007), suggesting that how a female apportions investment in egg production can affect her fitness.

In this study, I examined whether changes in egg volume and shape in an introduced population of song thrushes in New Zealand had any effect on a variety of fitness-related traits. I tested whether egg size and egg shape varied with clutch size, season, hatching success, daily egg mass loss (the result of water loss during embryonic development, Rahn & Ar 1974, which may affect hatching success, e.g., Reid *et al.* 2000), incubation behaviour, risk of desertion, nestling size and levels of brood reduction (i.e., nestling mortality). If changes in egg morphology are an adaptive response to the New Zealand environment, there should be little negative effect on fitness, and large eggs may even be selected against. On the other hand, it is possible that decreases in egg volume are the direct result of decreased body size in New Zealand, and I tested this hypothesis by comparing the body mass of thrushes in New Zealand with that in the native range.

4.3 Methods

Between 2003-2008, eggs were measured and weighed in a song thrush population nesting at Kowhai Bush, Kaikoura (see Chapter 1 for a description of the study species and map of the study site). Sampling effort was low in 2003-2005 (<5% of nests found in each breeding season) but increased in 2006-2008 (>50% of nests). I treated each clutch as an independent data point, based on the assumptions that separate clutches were laid by different females but the eggs within each clutch were laid by the same female. Egg length and maximum width were measured to the nearest 0.01 mm using digital callipers and I used these dimensions to calculate an index of egg volume and egg shape from the following formulas:

Egg Volume Index = 0.5 x Length x Width^2 (in cm^3, after Hoyt 1979)

Egg Shape Index = Length/Width

The volume index provides a value approximately equal to the actual volume, while the egg shape index is a measure of elongation: larger values indicate more pointed or elongated eggs, while low values indicate shorter and broader egg shapes. Egg volume and shape were not correlated (correlation test: $r = 0.04$, $df = 489$, $p = 0.38$), so I have treated the two measures of egg morphology as independent traits. During 2006-2008, a proportion of eggs were also weighed using a digital scale (accurate to the nearest 0.01 g). Fresh masses (i.e., pre-incubation) were recorded for 69 nests, and eggs from some nests were reweighed during the incubation period to estimate daily mass loss rates (absolute mass loss and percent mass loss); as daily mass loss remains relatively constant throughout the incubation period (Drent 1970), this should provide an appropriate measure for comparison. Only nests for which the data spanned at least 6 days were included (actual length of time ranged from 6 to 10 days), excluding the first two days of incubation. As egg volume and fresh egg mass are highly correlated (correlation test on the log-transformed means/clutch: $t = 19.1$, $df = 61$, $p < 0.01$, $r = 0.93$), I used volume as the measure of egg size.

I collected data on adult body mass by catching birds in mist nets and weighing them with a digital scale (to nearest 0.1 g). I only used birds caught and weighed over October-November, as this coincides with the main period of nesting. Using a t-test, I compared the body mass of song thrushes at Kowhai Bush with published estimates from Cramp (1988) for British song thrushes in the native range (74 g). Data on incubation behaviour were collected by filming nests for a six hour period (see

Chapter 5 for information on filming protocols). Females that were overly disturbed by the filming process spent an unusually long time away from the nest in the first hour of filming (i.e., > 30 minutes) and such films were excluded from the analysis.

Clutch size (the number of eggs laid per nesting attempt) was confirmed when the same number of eggs was present for two consecutive visits. Because of their scarcity, only four clutches of five eggs and 11 clutches of two eggs were measured, compared with 44 and 81 for 3- and 4-egg clutches, respectively. However, mean clutch size for nests with measured eggs and known clutch size was 3.56 eggs ± 0.058 (n = 140), which is the same as for all nests (3.56), so the ratio of clutch sizes measured here appears to be a representative sample of the population. Laying order (an egg's position within the sequence of laying for its clutch) was known for 41 clutches and 81 eggs, though the laying order of every egg within a clutch was not always known. Hatching success was defined as the proportion of eggs that hatched out of the total number of eggs present at hatching (i.e., not including eggs that were abandoned or predated during the incubation period) and data on brood reduction (individual nestling mortality) were gathered from successful nests where brood size and the number of fledglings were known (i.e., number hatched – number fledged). Hatchlings were weighed with a digital scale (to the nearest 0.01 g) and the left tarsus measured using digital callipers (to the nearest 0.01 mm). Nest outcome was defined as successful if at least one nestling fledged (or was 10+ days old, and thus ready to fledge, on the last visit), otherwise the attempt was classed as a failure, or 'unknown' if the nest was still active at the last visit. Failed nests were subdivided into those that failed as a result of nest predation (broken eggs, dead, mutilated chicks, or empty nests before fledging was possible), desertion (one or both parents abandoning the nest), or 'other' causes (usually poor nest construction).

Statistical tests were carried out in R 2.8.1 (R Development Core Team 2006). I used generalised linear models (GLMs; Crawley 2005) to analyse trends in egg morphology (volume and shape) with clutch size (as a factor), year, laying date (month of first egg) and laying order. All tests were also run on a restricted dataset containing only 2006-2008 nests (pre-2006, <10 clutches were measured per year), but as the results did not differ from those for the full dataset, only results from the full dataset are reported here. To avoid pseudoreplication (eggs from the same clutch are not independent), I used the nested procedure to test for significance; in R, the degrees of freedom are shown as if each egg were treated as independent, but the p-value has been calculated correctly, using

the residual degrees of freedom for 'clutch'. I used the mean volume/shape of eggs from each clutch in analyses related to outcome (success or failure) and egg mass loss rates, because eggs from the same clutch are not independent. Egg volume, shape and mass were all log-transformed to meet the assumptions of the statistical tests used. The incubation data (percent time spent incubating) and percent daily egg mass loss were both transformed using arcsine ($\sin^{-1}\sqrt{[0.01*p]}$) for testing against egg morphology in separate GLMs. Nest desertion was tested using a GLM with the distribution specified as binomial, so the appropriate transformation was performed within the test itself. To test whether egg morphology affected hatching success, I ran a GLM specifying a binomial distribution, separating nests where all eggs hatched (0) and those which contained at least one egg that failed to hatch (1). Brood reduction was tested using both a Poisson GLM (using the actual count data) and a binomial GLM (presence/absence of brood reduction in a nest). Means for variables with multiple values per clutch (e.g., egg volume, daily mass loss) were calculated from the mean of each clutch. All means are given ± standard error (SE).

4.4 Results

4.4.1 Effect of season and clutch size on egg morphology

Across all clutches, egg volume averaged 5.58 cm^3 ± 0.04 (n = 155; range: 4.12 to 7.31), while fresh egg mass averaged 5.88 g ± 0.06 (n = 69; range: 4.94 to 7.24). Differences in egg volume between clutch sizes were not significant ($F = 1.23$, $df = 3, 460$, $p = 0.30$), but there was a significant interaction between clutch size and the month in which an egg was laid on egg volume ($F = 5.30$, $df = 3, 457$, $p < 0.01$); as the season progressed, clutch size decreased and egg volume increased. Mean volume increased from 5.43 to 5.90 cm^3 over the breeding season and ranged from 5.40 to 5.70 cm^3 between clutch sizes. These differences amount to changes of 5-7% in egg volume. To control for season, I restricted my dataset to just clutches laid in October (the month in which I had the largest number of eggs and which corresponds to the peak in laying of first clutches). Egg volume in October varied significantly between clutches of different sizes ($F = 4.4$, $df = 3, 292$, $p < 0.01$), though there was a significant year:clutch size interaction ($F = 6.2$, $df = 3, 289$, $p < 0.01$). Egg volume was largest in 4-egg clutches and smallest in clutches of five eggs (Fig. 4.1a), while the significant interaction was the result of clutch size increasing and egg size decreasing slightly over the course of the study.

The egg shape index averaged 1.324 ± 0.005 (n = 155, range: 1.171 to 1.566). The interaction between month and clutch size was significant ($F = 4.74$, $df = 3, 457$, $p < 0.01$); eggs became more rounded as the season progressed (mean shape decreased from 1.349 to 1.319). Egg shape was similar for clutches of three and four eggs (1.325 and 1.320, respectively; Fig. 4.1b), but eggs from 2- and 5-egg clutches were more pointed (1.348 and 1.334, respectively); these differences between clutch sizes were marginally non-significant ($F = 2.49$, $df = 3, 460$, $p = 0.059$). Using data from October only, to control for seasonal effects, egg shape varied significantly between clutches of different sizes, after controlling for the non-significant effect of year ($F = 3.2$, $df = 3, 292$, $p < 0.05$).

There was no effect of laying order on either egg volume ($F = 1.36$, $df = 1, 93$, $p = 0.25$) or egg shape ($F = 0.78$, $df = 1, 93$, $p = 0.38$).

4.4.2 Effect of egg morphology on hatching success

Mean egg volume was not significantly different between deserted and non-deserted nests ($\chi^2 = 1.26$, $df = 1, 120$, $p = 0.26$), even when nests that failed due to predation were excluded ($\chi^2 = 0.42$, $df = 1, 81$, $p = 0.52$). Egg shape was also not related to nest desertion ($\chi^2 = 1.32$, $df = 1, 120$, $p = 0.25$).

There was no relationship between the mean egg volume of a clutch and whether any eggs failed to hatch in that clutch ($\chi^2 = 0.82$, $df = 1, 54$, $p = 0.37$), but mean egg shape was almost significant ($p = 0.069$) and became more significant after controlling for year and month of first egg ($\chi^2 = 3.57$, $df = 1, 52$, $p = 0.059$). Eggs in nests that suffered from hatching failure tended to be more pointed.

4.4.3 Effect of egg morphology on incubation behaviour and daily mass loss rates

There was a significant relationship between percent time spent incubating and egg shape ($F = 15.5$, $df = 1, 15$, $p < 0.01$). Incubation attentiveness was lower for eggs that were more pointed (Fig. 4.2).

On average, eggs lost 0.057 g ± 0.0029 per day, which is equivalent to a mean daily percent decrease in mass of 0.98% ± 0.054 (Fig. 4.3). However, there was no significant difference in daily mass loss of eggs between clutches of different sizes ($F = 0.60$, $df = 2, 16$, $p = 0.56$), and no relationship between mass loss (actual or percent) and egg volume (actual: $F = 0.35$, $df = 1, 17$, $p = 0.56$; percent: $F = 1.18$, $df = 1, 17$, $p = 0.29$) or egg shape (actual: $F = 0.01$, $df = 1, 17$, $p = 0.93$; percent: $F = 0.03$, $df = 1, 17$, $p = 0.88$). Although sample sizes were small, a t-test comparing daily

mass loss of 10 nests without hatching failure and 3 nests in which one egg per clutch failed to hatch found that mass loss was significantly higher in nests with hatching failure ($t = 2.3$, $df = 11$, $p < 0.05$).

4.4.4 Effect of egg morphology on nestling size and survival

Egg volume was significantly related to hatchling mass (Fig. 4.4a; $F = 9.60$, $df = 1, 25$, $p < 0.01$), with heavier nestlings hatching from larger eggs. There was no significant relationship between mean nestling tarsus length per nest and mean egg volume (Fig. 4.4b; $F = 0.05$, $df = 1, 25$, $p = 0.64$). Hatchling measurements were only gathered for one 5-egg clutch, so clutch size could not be included in either model; however, there was no significant difference between 3- and 4-egg clutches in either hatching mass ($F = 0.44$, $df = 1, 24$, $p = 0.51$), or hatching tarsus length ($F = 0.17$, $df = 1, 23$, $p = 0.68$).

Mean egg volume was not related to the number of nestlings per successful nest that died before fledging ($\chi^2 = 1.32$, $df = 1, 25$, $p = 0.25$), or the incidence of brood reduction ($\chi^2 = 0.60$, $df = 1, 25$, $p = 0.44$); however, mean egg shape was significantly higher (i.e., eggs were more pointed) in nests where brood reduction occurred ($\chi^2 = 3.87$, $df = 1, 25$, $p < 0.05$) and became more significant when clutch size was included first in the model (i.e., after controlling for clutch size; Fig. 4.5; $\chi^2 = 5.63$, $df = 1, 23$, $p < 0.05$), though the magnitude of brood reduction per nest (i.e., number of dead nestlings) was not related to egg shape ($\chi^2 = 1.07$, $df = 1, 25$, $p = 0.30$).

There was no relationship between nest outcome (i.e., at least one nestling fledged vs. none fledged) and mean egg volume of a clutch ($\chi^2 = 0.07$, $df = 1, 120$, $p = 0.80$) or mean egg shape ($\chi^2 = 0.08$, $df = 1, 120$, $p = 0.78$), even if nests lost to predation were removed from the dataset (volume: $\chi^2 = 0.04$, $df = 1, 81$, $p = 0.85$; shape: $\chi^2 = 0.72$, $df = 1, 81$, $p = 0.40$).

4.4.5 Adult body mass in New Zealand

Adult body mass of song thrushes in New Zealand appears to have decreased by ~ 4-5 g (7-8%) since their introduction. Mean body mass of female song thrushes during the breeding season averaged 69.0 ± 1.77 g (range: 60.2-77.3 g), while mean mass for a larger sample of males and females combined was 67.9 ± 1.10 (n = 21, range: 60.2-77.3 g). Compared to the mean of 74 g for song thrushes from Britain (Cramp 1988), New Zealand birds were significantly lighter ($t = -5.5$, $df = 20$, $p < 0.01$).

4.5 Discussion

I found some evidence for the effects of changes in egg morphology on offspring fitness in an introduced population of song thrushes in New Zealand. Egg volume was significantly related to nestling size at hatching, with larger eggs producing larger hatchlings, while egg shape was possibly linked to hatching failure, with more pointed eggs being less likely to hatch and females spending less time incubating clutches with more pointed eggs. Egg shape was also significantly more pointed in nests in which brood reduction occurred; however, neither egg volume nor shape was related to nest desertion. I found a tradeoff between clutch size and egg volume in October (i.e., controlling for seasonal effects), and there was a significant effect of clutch size on egg volume with timing through the breeding season; as the season progressed, clutch size decreased, whilst egg volume increased. Egg shape was also significantly different between clutch sizes when controlled for season, with eggs in 3- and 4-egg clutches being more rounded than eggs from 2- and 5-egg clutches, so eggs in the extreme clutch sizes are also at the extremes of egg shape, which may be suboptimal. Egg mass loss was not greater for larger clutches or related to egg volume or shape, but eggs at Kowhai Bush are possibly losing more mass than eggs from native British/European populations (see later) and this may have an effect on hatching success.

The pattern of decreasing clutch size and increasing egg size over the season has been found in other species (Perrins 1970, Styrsky *et al.* 1999). For example, Styrsky *et al.* (1999) found evidence that egg size was more important for the survival of late-season clutches of the house wren (*Troglodytes aedon*), which consist of fewer and larger eggs than earlier clutches, perhaps because food availability (and possibly also prey quality) was lower later in the season (Styrsky *et al.* 1999). However, supplemental feeding of nestlings (providing containers of mealworms at nest boxes) in the following breeding season only slightly increased nestling mass at fledging for early broods and had no effect on late broods, while there was a significant positive relationship between egg mass and nestling survival in early-season and nestling mass and size of both early- and late-season clutches (Styrsky *et al.* 2000). For great tits (*Parus major*), Perrins (1970) suggested that the cause of decreasing egg size over the season was not reduced food availability, but the result of a decrease in value of late-fledged young. Lower survival of late-fledged young selects for smaller clutches, whilst laying larger eggs is likely to increase nestling survival, even if only during the first few days of life

(which may be the most critical, e.g., Grant 1991). Perrins (1970) also suggested that *early*-laying birds may in fact be the ones limited by food availability, and may trade off laying larger eggs for laying earlier. Higher survival of early-fledged young appears to be common (Martin 1987, Naef-Daenzer *et al.* 2001), and nest success is higher early in the season at Kowhai Bush (Chapter 2), so early breeding attempts probably also produce more surviving offspring; thus, Perrins' (1970) suggestion is likely to be true for the population in this study. Food availability probably decreases over the season at Kowhai Bush, as earthworm availability decreases as the soil dries out, though this may have a greater effect on nestling survival than egg size.

Despite the low sample of unhatched eggs and the inclusion of causes of hatching failure not likely to be related to egg morphology (e.g., infertility, unless female quality links both traits), there was some suggestion that egg morphology plays a role in hatching success. Encabo *et al.* (2001) did not find any relationship between egg shape and hatching success in great tits or blackbirds (*Turdus merula*), whereas in my study song thrush clutches that contained unhatched eggs tended to be more pointed, which suggests that egg shape may affect hatching success. This is an area that would benefit from a focused study to collect more data on hatching failure and egg shape. A useful exercise would be to divide unhatched eggs into fertile and infertile eggs and then test for a relationship with shape in each group. If hatching failure in both groups is linked to egg shape, it would suggest that characteristics of the female may have more effect than shape *per se*. If shape is only important for fertile unhatched eggs, then characteristics of the egg itself may be causing embryo mortality. However, female quality may still be a confounding factor, as I also found differences in incubation attentiveness that were correlated with egg shape, with females spending less time incubating clutches of more pointed eggs.

Egg shape was also related to nestling survival, with eggs in nests where brood reduction occurred being significantly more pointed. Although the magnitude of brood reduction per nest was not related to egg shape, nestlings that died were possibly from the more pointed eggs within the clutch. Egg shape may affect the environment of the embryo, such as the efficiency of gas exchange or heat transfer (Gosler *et al*. 2005) and thus might have an important effect on embryo development, which could affect nestling quality in a way that parents are less able to compensate for than differences in hatchling mass. Alternatively, lower quality females may be less able to produce

optimally-shaped eggs and provide optimal levels of incubation, which could result in an apparent correlation between egg shape and fitness-related traits, such as clutch size and hatching success, when the true cause of both traits is female condition or age/genetic quality. Egg size does correlate with female condition in some species (e.g., herring gulls *Larus argentatus*, Risch & Rohwer 2000, great tits, Hõrak *et al.* 1995, starlings *Sturnus vulgaris*, Smith *et al.* 1993), but not all (Deeming 2007).

Differences in mass loss rates of eggs may also reflect female quality, or the quality of incubation and embryo development. Drent (1970), using data from a German study, calculated a daily loss rate of 0.051 g per day in a population of song thrushes with similar egg mass (5.80 g, vs. 5.88 g in this study at Kowhai Bush), while eggs in this study lost 0.057 g per day. In terms of the percentage mass lost, these amounts equate to 0.88% and 0.97% per day, respectively, or 11.8% and 14.3% over the incubation period (13.4 days in the European population, Groebbels & Möbert 1927, and 14.7 days at Kowhai Bush, Chapter 2). This suggests that eggs in the introduced population may be losing more mass than eggs in native British/European populations, perhaps as a result of differences in ambient temperature and humidity. Any effect it may have on hatching success and nestling condition is not clear, as low sample sizes for both mass loss rates and hatching success mean that it could not be properly tested here. Anecdotally, eggs from three nests where hatching failure occurred lost more mass (both absolutely and proportionally) than ten nests in which all eggs hatched. Thus, increased egg mass loss may be a factor driving the observed increase in hatching failure among introduced birds in New Zealand compared with Britain (Briskie & Mackintosh 2004). Future studies of egg mass loss (daily and total) would therefore be valuable to determine whether the viability of thrush embryos is being compromised by overly high rates of water loss. As water loss is related to porosity (Rahn & Ar 1974), there would also be value in studying features of the eggshell. It would also be useful to compare a population from a region with a different climate, such as higher summer rainfall, to assess what effect climate has on mass loss rates.

I have no data on the condition of adult birds or habitat quality at Kowhai Bush, but it seems likely that egg morphology is linked to female condition and/or body size in this population, because some clutch-level measures of egg morphology, such as mean egg shape per clutch, appear to be having an effect on offspring survival. However, paired measurements of female condition and egg morphology are required to confirm this. Egg shape was related to several fitness traits (e.g., hatching

success and brood reduction), which suggests that shape may be a better indicator of female condition than volume. Unlike egg shape, egg volume varied significantly between years, so environmental conditions may affect female condition, or the availability of resources for egg production. A greater time span of measurements is needed to identify any long-term trends in egg volume and broadening the study to include data on other egg traits, such as yolk mass and eggshell porosity, would be useful to assess whether variation in these traits affects offspring survival and condition. Swapping whole clutches between nests may also help to tease apart the effects of egg morphology and female quality.

Song thrushes at my study site were signficantly lighter than European birds and this difference could explain the decrease in egg size in New Zealand. Rahn *et al.* (1975) calculated family-specific equations to predict egg mass using body mass: Egg Mass = a(Body Mass)^b; for the family Turdidae, a = 0.317 and b = 0.691, so a body mass of 69 g predicts an egg mass of 5.91 g, which is very close to the fresh egg mass measured directly in this population (5.88 g). It seems likely that adult body mass is lower in New Zealand (~70 g, this study, Heather & Robertson 2000) than in Britain (74 g, Cramp 1988) and this could explain the decrease in egg size, as the two are of a similar magnitude (~7% decrease in egg volume and a 7-8% decrease in body mass). So it appears that the decrease in egg size in New Zealand may be a direct result of a decrease in adult body size and, therefore, potentially a non-adaptive consequence of changes in adult body size. It is not known why thrushes are smaller in New Zealand, although Bergmann's rule relates body size with ambient temperature, predicting that individuals in warmer environments (i.e., lower latitudes) will be smaller than those from colder regions (Murphy 1985). The change in body mass of song thrushes found in this study is in the predicted direction (birds are smaller in New Zealand, which is closer to the Equator than Britain and therefore warmer). It is interesting to speculate that if global warming causes temperatures in Britain to rise, song thrushes in the native range may become smaller as a result, and if such a change did occur it would be likely to cause a corresponding decline in egg size, though there is no evidence that this has occurred to date (Yom-Tov *et al.* 2006). The findings of this study suggest that such a decline may have negative consequences for offspring fitness.

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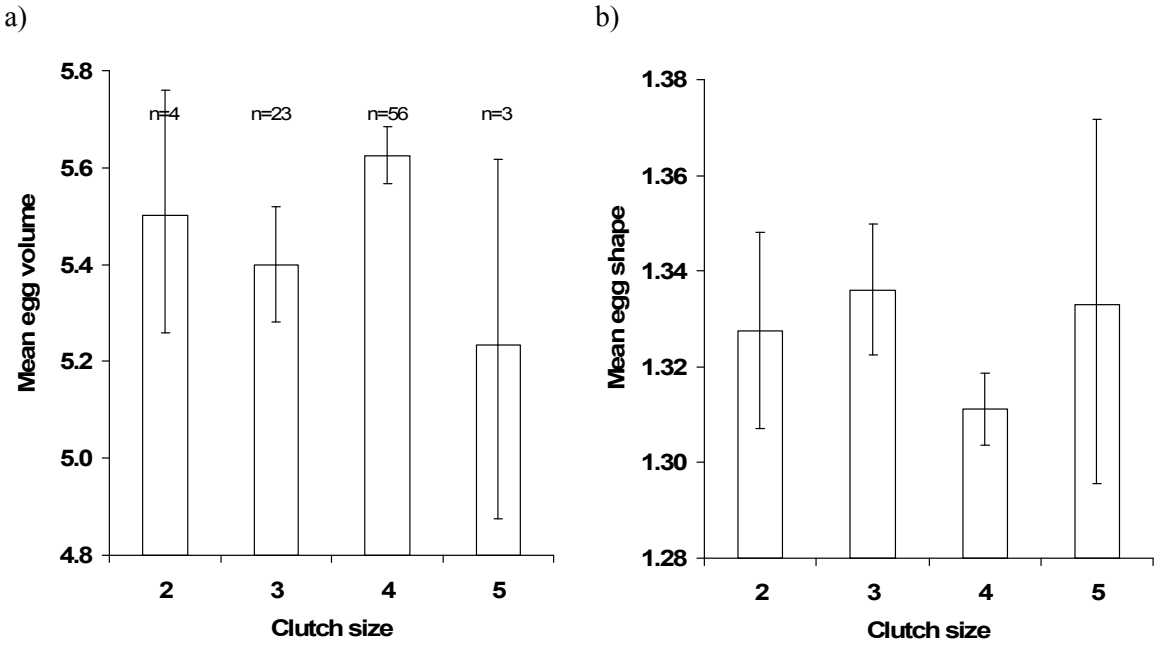


Figure 4.1. Mean a) egg volume (0.5 x Length x Width2) and b) egg shape (Length/Width) per clutch size for clutches laid in October (sample sizes are given above each group in graph a). There was no direct effect of clutch size on egg volume when considering data from all months, though there was a significant interaction between clutch size and month; as the season progresses, clutch size decreases and egg volume increases, while egg shape decreases. However, the differences in egg volume and shape between clutch sizes in October were significant.

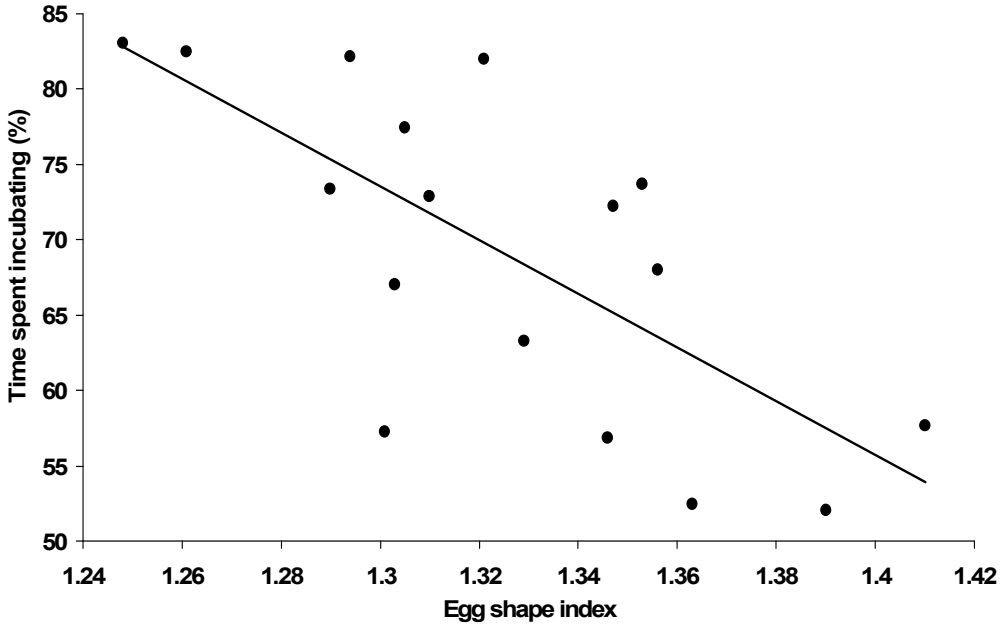


Figure 4.2. Time spent incubating (percentage of a 6-hour period) versus mean egg shape (Length/Width). Clutches of more-pointed eggs were given significantly lower levels of incubation.

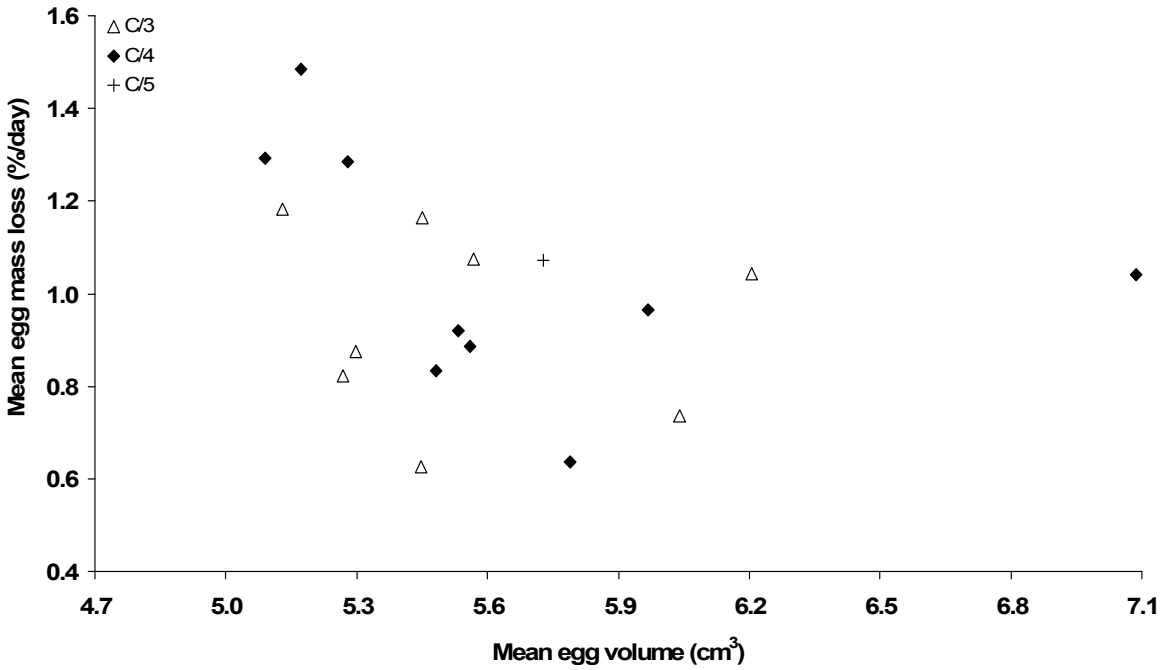
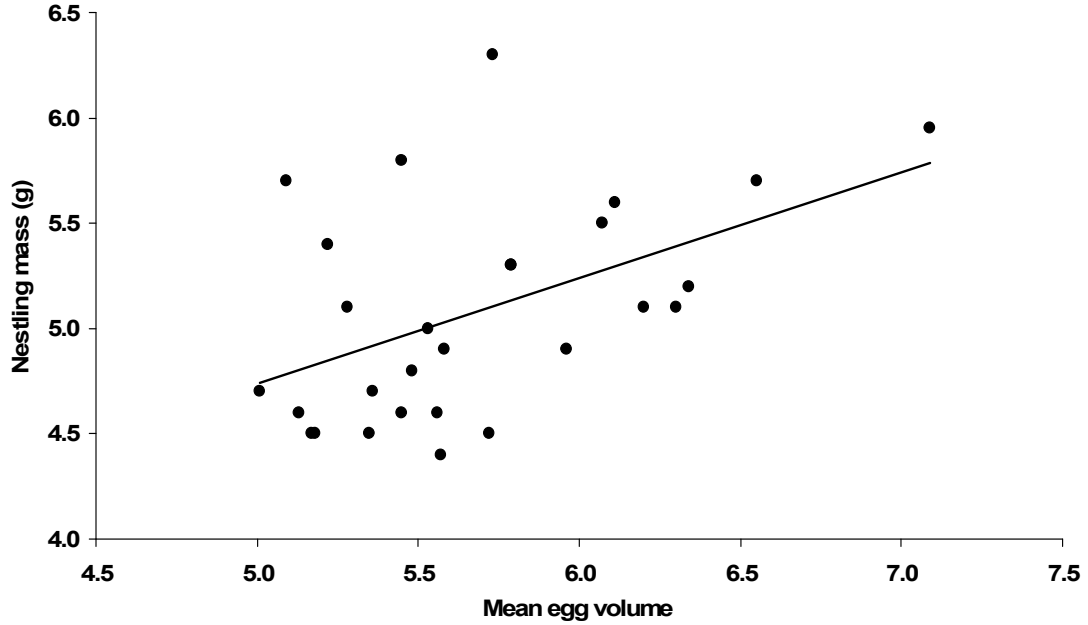


Figure 4.3. Mean egg mass loss per day, expressed as a percentage of fresh egg mass; differences were averaged from mass measurements spanning 6-10 days (the incubation period is typically 14-15 days). There was no difference in daily mass loss (long-transformed) with egg volume (mean/clutch) or clutch size (diamonds 3-egg clutches, triangles: 4-egg clutches, circles 5-egg clutches).

a)



b)

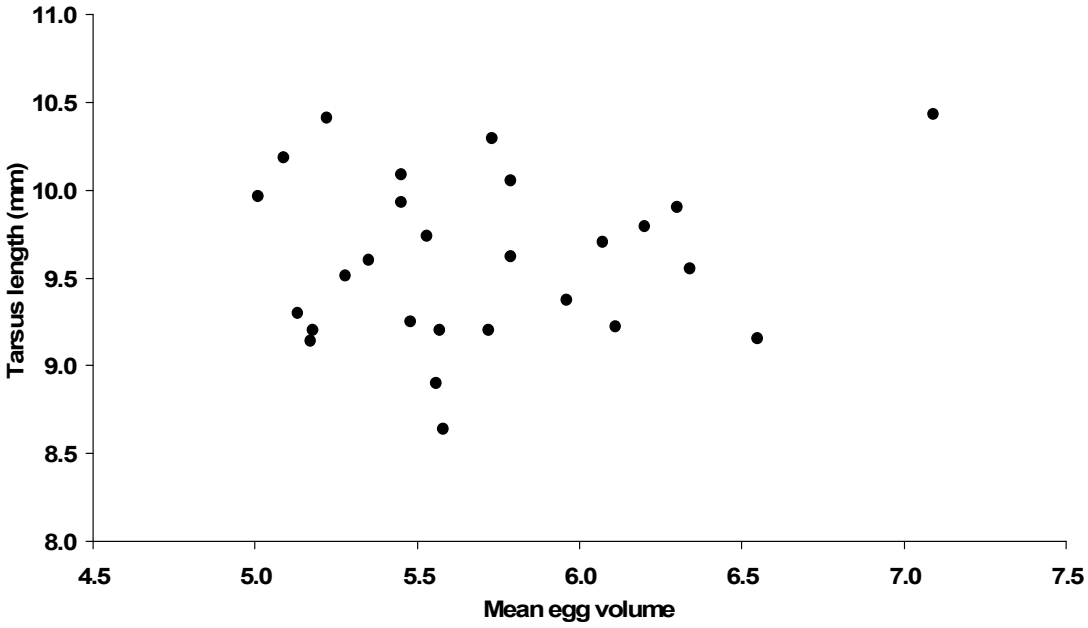


Figure 4.4. Mean hatchling mass (a) and tarsus length (b) per nest versus mean egg volume. Nestlings from larger eggs were significantly heavier, but there was no relationship with tarsus length.

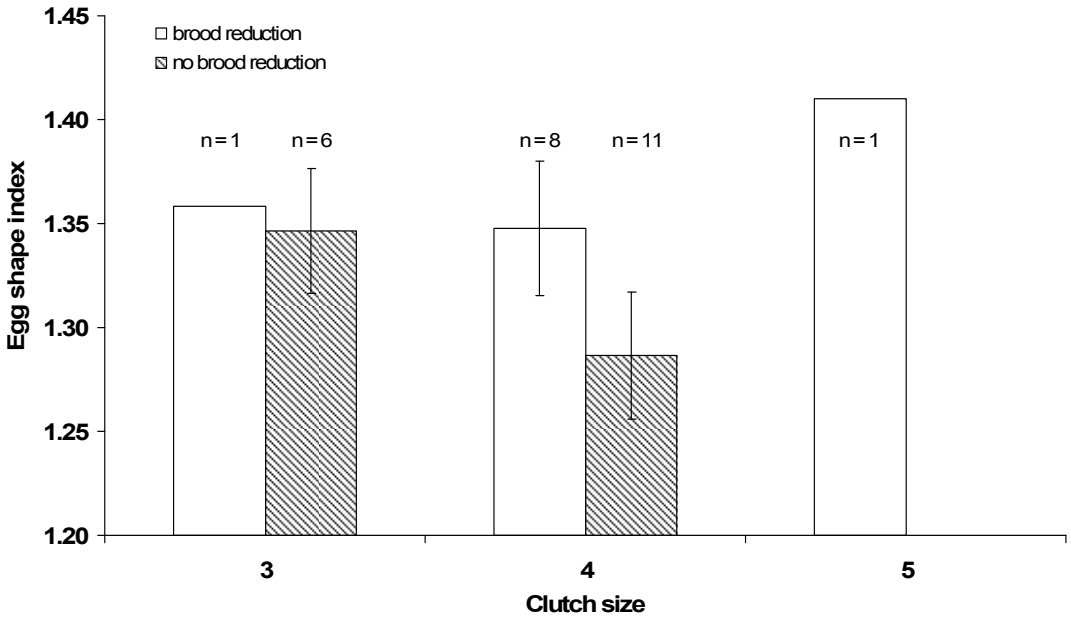


Figure 4.5. Mean egg shape (Length/Width) per clutch size for successful nests that experienced brood reduction between hatching and fledging (unshaded bars) and those in which all nestlings fledged (shaded bars). Egg shape was significantly higher for nests in which one or more nestlings died. No 5-egg clutches were successful; however, the nestlings of one clutch reached pin break (6-7 days old) and had lost one nestling within days of hatching, so was included here.

=== Chapter 5 ===

An experimental test of food limitation in the introduced song thrush (*Turdus philomelos*)

5.1 Abstract

Mean clutch size of song thrushes (*Turdus philomelos*) in New Zealand has decreased by about half an egg (12.5%) since their introduction from Britain in the mid 19th century. In contrast to the native range, thrushes in New Zealand are more likely to lay clutches of three and four eggs, while 5-egg clutches are rare. I studied clutch size and other life-history traits in a population of song thrushes at Kowhai Bush, Kaikoura, in order to determine if selection against 5-egg clutches can explain the decrease in clutch size among song thrushes in New Zealand. The number of eggs that hatched significantly increased with increasing natural clutch size from 2-4 eggs, but there was no further increase for 5-egg clutches. The number of fledglings varied only slightly between 3- and 4-egg clutches, with each producing approximately one fledgling per nest. None of five natural 5-egg clutches produced any fledglings, which suggests that 5-egg clutches do not have a higher reproductive success than smaller clutches. I then created 20 experimental clutches by adding or removing one egg/nestling and found no significant difference between the number of eggs hatched or fledglings produced for control, reduced or enlarged clutches, confirming that enlarged clutches did not increase reproductive success in this population. Females did not spend more time incubating larger clutches, but they did make more visits to nests containing experimentally-enlarged clutches, and off-bout length was shorter than for nests with smaller natural clutch sizes, suggesting some increased costs of incubating enlarged clutches. Nestling size was not significantly different between 3- and 4-egg clutches and there was no difference in growth rates of nestlings in experimental nests. Overall, my results indicate that 3- and 4-egg clutches, which accounted for >90% of all clutches found at Kowhai Bush, were equally the most productive and there appears to be directional selection against 5-egg clutches that may account for the decline of clutch size in this population of song thrushes since their introduction <150 years ago.

5.2 Introduction

Song thrushes (*Turdus philomelos*) in New Zealand currently lay fewer eggs per clutch than in their ancestral populations in Britain (Evans *et al.* 2005). Since their introduction in the mid-19th century, mean clutch size has decreased by ~12.5%, from ~4 eggs per clutch in Britain to ~3.5 eggs per clutch in New Zealand (Chapter 2). Although the modal clutch size is still four eggs for both populations, few females in New Zealand lay clutches of five eggs, while clutches of three eggs are more frequent than in Britain (Cramp 1988, unpubl. data). Clutch size also appears to have decreased throughout New Zealand for several other introduced passerine species, not just song thrushes (Evans *et al.* 2005). This change has occurred in a relatively short time (<150 years) and it is possible that selection is still occurring to further reduce clutch size. The reason for the decline in clutch size in song thrushes and other introduced birds is unknown, but studying these introduced populations may provide insight into the possible selective forces on clutch size evolution in general.

The factors determining clutch have long attracted the attention of ornithologists (e.g., Lack 1947, Skutch 1949, Ricklefs 2000, Jetz *et al.* 2008), and a huge literature has accumulated on the likely factors controlling clutch size in birds. The importance of food availability was first identified by Lack (1947, 1968) as a key selective force on clutch size in birds. Nevertheless, the energy requirements of egg production and incubation were considered minor compared with the demands of raising nestlings (though this is not the case, e.g., Thomson *et al.* 1998, Dobbs *et al.* 2006, Martin *et al.* 2007), so it was food limitation at the nestling stage that Lack (1947) proposed would act to increase or reduce clutch size. More precisely, he viewed clutch size as a product of natural selection in that individuals lay the number of eggs which corresponds to the number of offspring they can successfully raise. Thus, the most common clutch size in a population should be the one that produces the highest number of fledglings. This hypothesis has been refined over the years to incorporate models of clutch size that maximise reproductive success over a lifetime (e.g., Martin 2002, de Heij *et al.* 2006), and incorporate tradeoffs between offspring condition and number (e.g., Smith *et al.* 1989, Deerenberg *et al.* 1996, Hõrak 2003), as many studies have found that birds generally lay smaller clutches than they can raise during a single breeding attempt (e.g., Nur 1986, Engstrand & Bryant 2002, Martin 2002, Dobbs *et al.* 2006). Nonetheless, Lack's (1947) ideas provide a starting point for understanding changes in clutch size in introduced birds in New Zealand, and food limitation may in

fact be the main factor selecting for smaller clutches in the song thrush. For example, 29% of successful thrush nests at Kowhai Bush experienced brood reduction (i.e., nestling starvation; Chapter 2), suggesting that birds do struggle to provide sufficient nourishment for their young.

Nevertheless, food limitation may not be the only factor driving the decrease in clutch size of New Zealand song thrushes. Variation in population density, environmental variables (such as temperature), adult and juvenile survival and nest predation can also alter the benefits and costs of laying a certain number of eggs per clutch (e.g., Cooper *et al.* 2005, Wilkin *et al.* 2006, Dhondt 2001, Kleindorfer 2007). Given that most wild populations are subject to predation of both eggs and nestlings that may result in the loss of 50-90% of nests, it is not surprising that nest predation has also been suggested to play a key role in the evolution of clutch size, perhaps even overriding any effects of food limitation (Fontaine & Martin 2006). Skutch's (1949) nest predation hypothesis specifically considers the effect of predation on parental behaviour and how the likelihood of a predator finding a particular nest may be related to the level of activity at that nest. If predators are more likely to find a nest the more often the parents visit it, this could select for fewer visits and therefore restrict the amount of food that can be brought to the nest and the number of offspring that can be nourished. In turn, this will limit clutch size below the level that parents can raise, but which maximises offspring production once the risk of predation is taken into account. In a similar vein, Slagsvold (1984) proposed that high levels of nest predation (as well as other causes of nest failure, such as severe weather events) select for reduced investment in each clutch. He found that great tits (*Parus major*) with enlarged broods took longer to re-nest than those with reduced broods and they also produced fewer fledglings from the replacement clutch (Slagsvold 1984). Nest failure rates of introduced birds in New Zealand are relatively high (~65%; Chapter 2), so this could also be an important factor driving selection for reduced clutch size. If predation affects larger clutches disproportionately, then this should likewise favour a reduction in clutch size to minimise predation rate and maximise offspring production.

In this chapter, I used both observational and experimental data to determine the most productive clutch size in an introduced population of song thrushes in New Zealand. I compared the number of hatchlings and fledglings produced for each clutch size from natural nests and from nests in which I experimentally manipulated clutch and brood size. My experiment tested whether song

thrushes were capable of incubating an enlarged clutch and/or raising an enlarged brood, in order to assess whether decreased reproductive success could explain why the frequency of larger clutches is lower in New Zealand. In this experiment, I tested the ability of females to incubate larger clutches by comparing the time spent incubating for natural and experimental nests. I assessed the ability of parents to raise larger broods using nestling measurements (from natural and experimental nests) and parental feeding rates (from natural nests only). If clutches of five eggs are rare because there is selection acting against such large clutches, I expected parents to struggle with raising an additional nestling or even an additional egg; if this were so, I expected either a decrease in levels of incubation attentiveness (% time spent incubating), increased rates of hatching failure and brood reduction, and/or decreased nestling growth rates/body mass in experimental nests. If no directional selection was occurring, then 'enlarged' nests should produce more hatchlings/fledglings and there should be no difference between experimental and natural nests for any of the variables measured.

5.3 Methods

Clutch and brood manipulation experiments were undertaken at Kowhai Bush, Kaikoura (42º23'S, 173º37'E), over three breeding seasons (2006-2008). Chapter 2 provides a description of this field site and its song thrush population. In brief, the forest is situated on the floodplain of the Kowhai River and dominated by kanuka (*Kunzea ericoides*) trees in the younger, least-developed soils, where song thrushes are most abundant. A medium-sized (70 g) passerine, the song thrush feeds on invertebrates and fruit (Cramp 1988). Females build the nest and incubate the clutch without assistance from the male, then both parents provision the nestlings, with the male providing the bulk of the food, while the female also broods the young (Cramp 1988). After fledging, offspring are fed by their parents for a short time, before dispersing from their natal site. The female may start building a new nest while the male is still feeding fledglings (Cramp 1988).

5.3.1 Nest monitoring

Nests were monitored at Kowhai Bush from 2002-2008, although most of the data reported here were collected in the last three years of the study. Chapter 2 provides a detailed description of nest monitoring protocols. Briefly, nest searching was most intensively undertaken in a 15-ha area within

the forest and consisted primarily of a systemic search of the vegetation for nests (see Chapter 1, Fig. 1.1, for a map of the study area). This was the most effective method for finding the relatively large nests of song thrushes, as birds are shy and avoid humans. The majority of nests were monitored from discovery to the final outcome: success (fledging at least one chick) or failure (nest abandonment or the total loss of eggs or nestlings as a result of predation, nestling starvation, poor nest construction, or severe weather events). Nests were revisited every 2-3 days, in order to follow nest progress as accurately as possible whilst limiting disturbance, though daily visits were made as laying, hatching and fledging approached. Clutch size was confirmed when the same number of eggs was present for two visits. The number of eggs hatched was recorded for all nests where clutch size and hatching success (the proportion of eggs that hatched out of the total number of eggs present at hatching) was known, or assigned a zero value if the nest was predated before hatching. The incubation period was counted from the day the last egg was laid until the day the last egg hatched, and the nestling period from the day the first egg hatched until the day the last nestling fledged. Brood size was defined as the number of nestlings in the nest after all eggs had hatched. The number of fledglings (0-4) was known for 319 nests where clutch size was also known. To avoid additional disturbance at the nest, no attempts were made to catch adult birds, as this may have affected parental feeding rates or caused birds to abandon the nesting attempt. As a result, no measures of adult condition were available and it was not possible to identify individuals or distinguish between the male and female of a pair.

5.3.2 Clutch- and brood-size experiments

In 2006, triads of nests of the same age (i.e., all three clutches completed within one day of each other) were randomly assigned to one of the three treatment types: control, reduced and enlarged. Because natural 2- and 5-egg clutches were rare, only 3- and 4-egg clutches were used in the following experiments. The enlargement experiments were conducted on triads of both clutches and broods. Two days after incubation had begun (for brood experiments, two days after hatching was complete), two randomly-chosen eggs (nestlings) were taken from the 'reduced' nest; one was added to the 'enlarged' nest and the other switched with an egg (nestling) taken from the control nest. These translocations were all completed within 10 minutes and each treatment nest received a new egg/nestling to control for the possible effects of a foreign egg/nestling being added to the nest and for the effects of my

visitation to nests and handling of eggs/nestlings. Active nests manipulated during incubation were filmed halfway through incubation (see section 5.3.3 for a description of the protocol used here). Nestlings were then weighed and the left tarsus measured at hatching (<1 day old) and at feather pin-break (6-7 days old; day of pin break was taken to be the day that 1-2 mm of feather tip were exposed). I was not able to match a nestling from the egg it hatched and so both the native and foreign nestlings were treated together. Brood sizes also followed the pattern of reduced-control-enlarged, unless hatching failure occurred in any of the nests. Nests were re-filmed at pin break.

As the number of nests of the same age was low at any given time, I modified the experimental design in 2007 and 2008. Instead of triads, I used pairs of nests of the same age in which one nest was assigned to a reduced treatment and one nest to an enlarged treatment. Eggs/nestlings were transferred into 'enlarged' nests temporarily and returned to their source nests after two days. This allowed me to measure the short-term behavioural responses of adults to clutch/brood alterations both before and after within the same nest and thus reduced the total number of nests required for the experiment. 'Enlarged' nests were also created in 2008 by adding eggs from abandoned nests into nests of unknown age or when no other active nest was the same age (i.e., these nests were unpaired) to increase sample sizes. A third 'control' nest was also assigned at this time; although no eggs/nestlings were swapped from these nests because of the slight age differences, these nests did experience the same level of disturbance as experimental nests (e.g., visitation rate, egg handling). Nests manipulated during incubation were filmed approximately 5-7 days into the incubation period (see section 5.3.3 on filming protocols), then an egg was taken from one nest ('reduced') and placed into the other nest ('enlarged'); brood manipulations were carried out at pin break (about half way through the nestling period). After two days, the nests were re-filmed and the eggs/nestlings returned to their original nests.

To determine how my clutch/brood manipulations affected parental behaviour, I filmed nests both before and after the manipulation. Each nest was filmed twice to provide a within-female control for the experiment, and to test for differences in female behaviour between the two films. For 11 nests filmed between 2006-2008, I was also able to compare the mean time females spent away from the nest between incubation bouts ('off-bout length', measured in seconds) for natural clutch sizes. I excluded off-bouts where the female had been flushed and only used nests where disturbance was minimal (the female was not flushed more than once and/or she returned within five minutes of being flushed).

As changes in brood size may lead to changes in nestling condition and growth, I measured and weighed nestlings before and after brood manipulation. Only two experimental broods were filmed twice, so it was not possible to carry out statistical analysis on feeding rates, but I was able to compare growth rates and nestling mass/tarsus length between experimental broods and control nests (broods of the same clutch size and approximately the same age) to indirectly assess the ability of parents to feed experimentally-enlarged broods. Because experimental sample sizes were low, I also included clutch manipulations as experimental nests for these traits.

Control nests for non-film data (e.g., number of eggs hatched, nestling mass) were not necessarily the same nests for each trait measured, because not all data were available for all nests (whether experimental or natural). Hence, some control nests were not exactly the same age, but as close in age as was available (to control for seasonal effects). A further constraint on the experiment was that nests and eggs could not be completely randomly chosen. Nests in locations that made filming difficult were not used and eggs that looked too dissimilar (in size or patterning) were avoided in my egg-switching experiments, as there is a high risk of rejection of dissimilar eggs (Hale & Briskie 2007). Several nests were also excluded from the experiment as a result of equipment problems, adverse weather conditions, desertion or excessive distress displayed by the parent(s), or predation during the experiment. I also assumed there was no difference in behaviour between the two filming events, either due to the effects of repeated filming or natural changes in incubation levels over the incubation period. Females incubate for a lower percentage of time in the first few days of incubation, before they settle into a 'routine' (perhaps after recouping the energy spent on egg production), then for longer in the couple of days before hatching (*pers. obs.*); because the start and end of the incubation period were avoided and the time span of the experiment was short (two days), the assumption of no difference seems reasonable.

5.3.3 Measuring parental incubation and feeding behaviour using nest films

In 2002-2007, nests were filmed using analogue video cameras stationed a minimum distance of 10 m from the nest, for a period of six hours. To standardise for time of day, all films were started within 30 minutes of sunrise. Tapes were set on long play and ran for three hours, so nests were revisited three hours after the start of the session to change the tape. In 2008, nests were filmed using digital video

cameras which could record for the full six hours, so nests were not disturbed partway through filming. In order to account for differences in disturbance, 10 minutes at the start or on either side of the tape change were removed when females were flushed as a result of activity around the camera.

Nests containing eggs were filmed at mid-incubation (6-10 days after clutch completion) so that females had settled into typical incubation behaviour. However, some nests were filmed outside this period (i.e., those of unknown age), so nest age was included as a variable in analyses ('early', 0-5 days, 'mid', 6-10 days, or 'late' incubation, >10 days). These data were used to estimate number of visits (by the female or the combined number for both parents), the time spent incubating (incubation attentiveness) and off-bout length (the length of time females spent away from the nest). For most visits, I was able to determine the individual's sex by its behaviour at the nest or its size (males are slightly larger). Nests containing nestlings were filmed to collect data on parental feeding rates, number of visits (by both parents) and number of chicks fed per visit. Nests from previous years (2001-2005) had also been filmed using the same protocols, so these nests were also included in this study. The clutch/brood sizes of filmed nests ranged from 3-5 eggs and 2-4 nestlings.

In order to minimise disturbance, nests were filmed no more than twice during each nesting stage (incubation and nestling). If the second recording was compromised in any way (e.g., equipment malfunction, incorrect operation, etc.), a third filming was not attempted. If a female was unduly distressed by filming, no subsequent films were made of that nest. Nests subjected to manipulation (movement of either eggs or nestlings) were also only used once.

5.3.4 Statistical Analysis

Statistical tests were carried out using R 2.4.0 (R Development Core Team 2006). Data from unmanipulated nests on the number of eggs hatched and fledglings produced per nest were used to compare overall reproductive success of the different natural clutch sizes. To test these count data, I used generalised linear models (GLMs; Crawley 2005) and specified a quasi-Poisson distribution (as the data were overdispersed) to compare mean number of eggs hatched and mean number of fledglings produced per nest, with respect to clutch size. I included all nests where the number of eggs hatched and/or the number of nestlings fledged were known; i.e., these data include those nests that were depredated or abandoned before reaching either stage. For experimental nests, sample sizes were too

low to allow analysis on separate clutch sizes, so I combined the nests into groups according to treatment type, which created three groups: 'reduced' (N-1, where 'N' is the natural clutch size of the nest), 'control' (N) and 'enlarged' (N+1). For two 'enlarged' nests, where eggs from abandoned nests were added, the hatching and fledging success of the additional eggs were unknown, so in order to be conservative, I have assumed that both of these hatched and fledged and therefore I added two 'hatched' eggs and two 'fledglings' to the dataset. This had no significant effect on the differences between the groups.

Four variables recorded from nest films were log-transformed in all analyses: off-bout length, the number of visits per hour, feeding visits per hour and feeds per nestling per hour. Despite being a percentage, incubation attentiveness was approximately normally distributed and transformations did not improve the fit of the model, so the raw data were used in all tests. For the first step in analysing these data, I ran generalised linear models (GLMs) including multiple predictors: year, month of first egg (i.e., a measure of timing within the season), age (incubation films were aged as early, mid, or late incubation, estimated once eggs hatched; for nestling films, I used nestling age, in days) and clutch size (as a factor, because differences between clutch sizes were not necessarily linear). Most of the minimal adequate models contained only clutch size, unless no factor was significant, so I have only presented the results of single-factor analysis of variance (ANOVA) or of GLMs when variables besides clutch size were significant. I ran paired t-tests on the data from the repeated sampling of each nest (experimentally-enlarged vs. natural clutch size) to test the effect of clutch enlargement on incubation behaviour. Because I expected clutch enlargement to increase the stress of incubation on females, I ran one-tailed t-tests; however, I have only reported the statistical results for these tests where they differed from the results of two-tailed tests, which are more conservative.

For nestling mass and tarsus length, I used log-transformed data and ran unpaired t-tests to compare experimental with control measurements. I compared 'reduced' and 'enlarged' nests, as well as control and 'enlarged' nests, as the number of 'reduced' nests was small. The variances of some paired test groups were not equal, so I also used R's two-sample t-test for unequal variances, which calculates degrees of freedom for the test based on the sample sizes of each sample (note, the adjusted degrees of freedom may be non-integer values). For natural nests, I used ANOVA to test for

differences between clutch sizes. As 2- and 5-egg clutches were rare and nestlings from these clutches even rarer, no nestlings were measured at pin break for either clutch size.

5.4 Results

5.4.1 Reproductive success in nests with natural clutch size vs. experimentally-manipulated clutches

There was a significant difference in the number of eggs hatched per nest between clutches of different sizes (Fig. 5.1; $F = 7.14$, $df = 3, 324$, $p < 0.01$), with larger clutches generally producing more hatchlings. The number of natural 5-egg clutches was small ($n = 5$), so the lack of a difference in the number of eggs hatched in 5-egg clutches compared with any other clutch size may be a result of the low sample size. Clutches of three and four eggs produced approximately twice as many fledglings as clutches of two and five (Fig. 5.1), which was significant (Poisson GLM, taking account of overdispersion in the data: $F = 2.81$, $df = 3, 315$, $p < 0.05$).

Although 'enlarged' nests contained one extra egg and 'reduced' nests one less egg, there was no significant difference in the number of eggs hatched between 'reduced', control and 'enlarged' nests (Fig. 5.2; $F = 0.20$, $df = 2, 28$, $p = 0.82$). The number of nestlings fledged was also not significantly different between the three groups ($F = 0.22$, $df = 2, 41$, $p = 0.80$).

5.4.2 Incubation behaviour

There was a significant difference in the total number of visits per hour that adult birds made to clutches of different sizes, after controlling for the effects of year and timing within the season (Fig. 5.3a; $F = 4.45$, $df = 2, 23$, $p < 0.05$). Fewer visits were made to clutches of five eggs than to either 3- or 4-egg clutches, which had similar visitation rates. The number of visits made solely by the female followed the same pattern, though the difference between clutch sizes was less and no longer significant ($F = 2.75$, $df = 2, 24$, $p = 0.08$). Incubation attentiveness was highest for 4-egg clutches and lowest for 5-egg clutches (Fig. 5.3b); the difference between 3- and 4-egg clutches was significant after controlling for timing within the season (GLM: $F = 6.45$, $df = 2, 24$, $p < 0.01$), but the difference between 4- and 5-egg clutches was not, no doubt because of the low sample size for 5-egg clutches ($n = 2$). The length of time females spent away from the nest between incubation bouts (off-bout length) decreased significantly with nest age ($F = 17.6$, $df = 1, 8$, $p < 0.01$) and was significantly different

between clutch sizes (Fig. 5.3c), whether controlling for age ($F = 10.7$, $df = 2, 6$, $p < 0.05$), or not ($F = 5.52$, $df = 2, 7$, $p < 0.05$). Clutches of five had the longest off-bouts and there was no difference in off-bout length for 3- and 4-egg clutches, though there was more variability for 3-egg clutches.

There was no significant difference in the number of visits per hour between the natural and enlarged clutch sizes (Fig. 5.4; $t = -1.27$, $df = 4$, $p = 0.27$), but females made significantly more visits to the nest when it contained the experimentally-enlarged clutch size ($t = -2.64$, $df = 4$, $p < 0.05$, one-tailed test). There was no significant difference in the time spent incubating between the natural and enlarged clutches (Fig. 5.4; $t = -0.62$, $df = 4$, $p = 0.57$), but off-bout length was significantly higher for natural clutches ($t = 4.77$, $df = 3$, $p < 0.05$), i.e., females spent longer away from the nest with their natural clutch size.

5.4.3 Feeding behaviour (natural nests)

The number of visits per hour increased significantly with increasing brood size (Fig. 5.3d; $F = 7.03$, $df = 1, 31$, $p < 0.05$), as did the number of feeding visits per hour ($F = 10.46$, $df = 1, 32$, $p < 0.01$). The average number of feeds per nestling per hour was significantly related to nestling age ($F = 6.25$, $df = 1, 22$, $p < 0.05$); after controlling for year and nestling age (in days, range 7-9), brood size was almost significant ($F = 3.83$, $df = 1, 21$, $p = 0.064$). Older nestlings received significantly more feeds per hour, while the number of feeds per nestling increased slightly with brood size.

5.4.4 Nestling size at hatching and pin break

There was no difference in hatchling mass or tarsus length for chicks from natural clutches of different sizes (3-5 eggs; mass: $F = 2.2$, $df = 2, 23$, $p = 0.13$; tarsus: $F = 0.97$, $df = 2, 23$, $p = 0.39$). Hatchlings were significantly heavier in nests with experimentally-reduced clutch sizes (5.4 g in 'reduced' nests vs. 4.8 g in 'enlarged' nests; $t = 3.13$, $df = 3.9$, $p < 0.05$). Hatchling tarsus length was also greater in 'reduced' nests, though this difference was not significant (9.87 mm vs. 9.45 mm; $t = 2.23$, $df = 4$, $p = 0.09$).

There was no significant difference in mean nestling mass at pin break between natural nests of differing clutch sizes ($F = 1.18$, $df = 1, 29$, $p = 0.29$), though nestlings from clutches of three eggs tended to be slightly larger than those from 4-egg clutches (33.87 g vs. 31.29 g). Nestlings in 'reduced' nests were slightly heavier than those in 'enlarged' nests (35.9 g vs. 34.8 g), and nestlings in

'enlarged' nests were heavier than control nestlings (31.6 g), but neither difference was significant (reduced vs. enlarged: $t = 0.45$, $df = 6.7$, $p = 0.67$; enlarged vs. control: $t = -1.79$, $df = 15.19$, $p = 0.09$).

Mean nestling tarsal length was not significantly different between nestlings in clutches of different sizes ($F = 0.35$, $df = 29$, $p = 0.56$), though the difference between nestlings in 'enlarged' vs. control nests was almost significant (28.87 mm vs. 27.32 mm; $t = -2.07$, $df = 11.7$, $p = 0.06$).

5.5 Discussion

Larger clutches of song thrushes in New Zealand do not appear to produce more fledglings. Even for natural nests, the number of fledglings per nest did not vary significantly with increasing clutch size, such that clutches of three and four eggs produced, on average, roughly the same number of fledglings, which was four times the number of fledglings that was produced by 2-egg clutches. No nestlings fledged from five observed clutches of five eggs. The low numbers of 2- and 5-egg clutches mean that chance events, such as predation, have a greater influence on the exact numbers and outcomes for these clutches. However, there appears to be strong stabilising selection against both extremes of clutch size. Both the observational and experimental data show the same patterns of similar reproductive success and nestling condition (as measured by nestling mass and tarsus length at pin break) for 3- and 4-egg clutches and very low success for 2- and 5-egg clutches. Thus, selection appears to be favouring 3-egg clutches, as this clutch size produces the highest number of fledglings relative to the costs of reproduction. In other words, laying larger clutches of four or five eggs does not lead to greater reproductive success, as no additional young are produced, yet females must pay additional costs in egg production and the length of the laying period.

There was considerable variability in incubation attentiveness between females, but attentiveness was significantly higher for natural 4-egg clutches than for clutches of three (the difference was not quite significant for 4- vs. 5-egg clutches), while off-bout length (highest for 5-egg clutches) was also significantly different. Females did not consistently increase the time they spent incubating enlarged clutches compared with natural clutches, though there was a decrease (not significant, probably due to the low sample size of two nests) in the time spent incubating for reduced clutches. Visits to the nest were significantly more frequent during the experimental filming, irrespective of treatment group (enlarged or reduced), and off-bout length was shorter. Hence, despite

its conservativeness (the additional costs incurred during the experiment would have been significantly lower than if females had laid an extra egg and incubated it for the entire incubation period), the experiment appears to have induced females to modify their behaviour, though not all responded by changing incubation attentiveness. Whether constrained by food availability or nest predation, it appears that females do not increase incubation attentiveness for 5-egg clutches (even females who did not pay the cost of laying the extra egg did not), which may increase the costs of incubation by requiring the female to expend more energy maintaining the temperature of the eggs, or by slowing embryo development, so that the length of the incubation period is increased (Engstrand & Bryant 2002, Dobbs *et al.* 2006, Martin *et al.* 2007).

There was no increase in hatching failure (i.e., no difference in the number of eggs hatched between experimental and control nests), so females were apparently able to incubate enlarged clutches, but it is not known whether they paid any additional cost for this. Incubation periods may have been longer for enlarged clutches, but there was not enough data to properly test for a difference between 'enlarged' nests and natural nests. On the other hand, the ability of parents to raise enlarged broods is uncertain. The high incidence of brood reduction in this population (29% of successful nests, including those where brood size was already less than clutch size as a result of hatching failure), suggests that birds already struggle to raise the full clutch. Nevertheless, there was no significant difference in nestling mass/tarsus length at pin break between natural clutch sizes (3- vs. 4-egg clutches), and nestlings in experimental nests were actually heavier than those in control nests; a non-intuitive pattern which Dobbs *et al.* (2006) also found for house wrens that incubated enlarged clutches. Similar feeding rates for all brood sizes (2-4; natural nests only) also suggests that pairs are probably not having difficulty feeding large clutches, though these results may be confounded by several factors (e.g., parental quality), and I was not able to collect sufficient experimental data on feeding rates to control for such factors. Brood reduction generally occurred before pin break (unpubl. data), so all data on feeding rates of broods with four nestlings were from pairs that successfully raised their full clutch to pin break, whereas broods of three were either from 3-egg clutches (i.e., full clutches) or 4-egg clutches that had lost an offspring through hatching failure or nestling mortality. Thus, feeding rates from earlier in the nestling period may be useful to determine whether differences in feeding rates are more pronounced between nests that experience brood reduction and those that

have 100% fledging success. My data also do not show the effect of the three treatments on the parental birds. It may be that parents are assuming the additional costs (or benefits) of changes to clutch/brood size, as has been found in other species (Thomson *et al.* 1998). Alternatively, the experiment may have been too conservative in nature to raise costs to the extent that parents were disadvantaged beyond the duration of the experiment.

Laying a larger clutch incurs costs throughout the nesting attempt (Deerenberg *et al.* 1996, Thomson *et al.* 1998, Dobbs *et al.* 2006). For example, the costs of egg production are increased and, as song thrushes lay one egg per day, larger clutches increase the laying period and expose the nest to predation for a longer period. From my data, it appears that birds laying 3-egg clutches gain the most benefit with the least cost. Unfortunately, sample sizes were low, so a more detailed analysis of these data was not possible. There were also other variables which may be relevant but were not measured, such as female condition, and I was also unable to differentiate between first and second broods or clutches laid by the same female. Additionally, I have controlled for seasonal effects without being able to look at these effects on their own. In Britain, mean clutch size also declines over the season (Cramp 1988), so this is not a point of difference with New Zealand, but it is not known whether the rate of decline is the same for both populations.

While my results cannot pinpoint causes for the selection against extreme clutch sizes, and against 5-egg clutches in particular, there is some additional evidence that food limitation is an important factor. Quantifying food availability for song thrushes is complex, because they often forage outside their territories (Cramp 1988), but rainfall levels provide a useful indicator, as their main food is earthworms and rainfall/soil moisture affects the depth of earthworms in the soil (Gerard 1967). Rainfall at Kowhai Bush is low (< 1 m annually) and relatively consistent throughout the year, though more usually falls in winter, and the soil moisture deficit peaks in summer (NIWA 2009), so the availability of earthworms, as well as other invertebrates that make up their diet, may be restricted during breeding. Intraspecific competition may also be more important in New Zealand than in Britain, as many introduced species exist at higher densities in New Zealand (MacLeod *et al.* 2005) and this could cause food limitation. Hence, further studies at Kowhai Bush would be useful to tease apart the cause(s) for selection against larger clutches. For example, providing supplementary food for

nestlings and/or adult birds to test for increased nestling condition and survival in supplemented nests, or increased incubation attentiveness for food-supplemented females.

There is also considerable scope for future research into the decline in clutch size of song thrushes in other introduced populations. Song thrushes have been introduced to other countries (e.g., Australia), which makes it possible to study multiple introduced populations to determine if similar changes have occurred separately in these populations, or if there are any populations where clutch size has increased. Research could also extend to other introduced species, such as blackbirds (*Turdus merula*), a close relative to the song thrush, or less closely related species, such as the seed-eating finches (e.g., the goldfinch *Carduelis carduelis*, or chaffinch *Fringilla coelebs*, which feeds its offspring insects), for which other factors may be comparatively more important for clutch size, and yet clutch size appears to have decreased for these species as well (Evans *et al.* 2005).

In summary, song thrushes at Kowhai Bush are laying smaller clutches than birds from the original source populations in Britain. There appears to be directional selection against extreme clutch sizes (two and five eggs), as intermediate clutch sizes (three and four eggs) produce, on average, approximately four times the number of fledglings. There was no effect of experimentally increasing or decreasing clutch size on incubation attentiveness, but females made more visits to nests containing the experimental clutch size, and off-bout length was shorter than for nests containing the natural clutch size. The number of fledglings produced per nest was not significantly different between experimental groups, with 'reduced', control and 'enlarged' nests all producing approximately the same number of fledglings. Hence, song thrushes at Kowhai Bush pay extra costs, but receive no benefits from laying 5-egg clutches.

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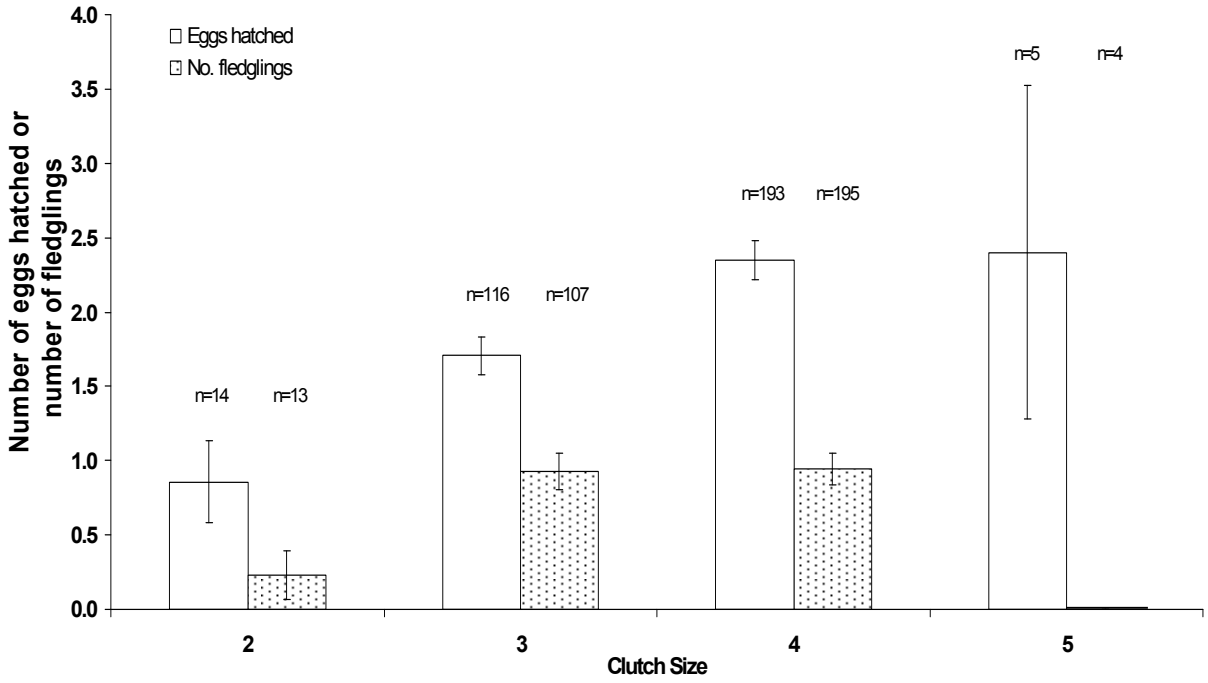

Figure 5.1. Mean (± SE) number of eggs hatched (unshaded bars) and number of fledglings (shaded bars) per nest in relation to natural clutch size. Included are all nests where number of hatchlings/fledglings was known and nests that failed before hatching/fledging (sample sizes are stated for each group).

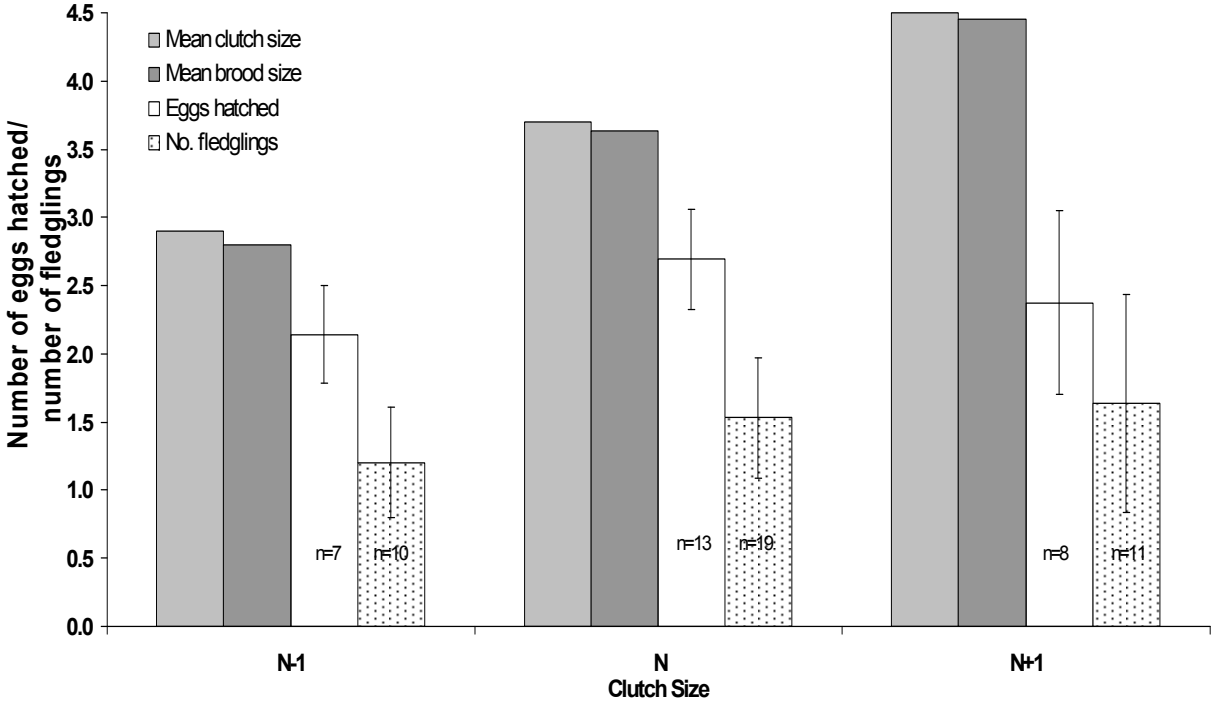

Figure 5.2. Mean (± SE) number of eggs hatched (unshaded bars) and nestlings fledged (dot-shaded bars) per nest, for reduced (N-1), control (N) and enlarged (N+1) nests. Because sample sizes (stated on the graph) were low, clutch/brood sizes were combined in these categories, so mean clutch size and mean brood size are shown on the left of each group. Despite 'reduced' nests containing one fewer egg and 'enlarged' nests one extra egg than control nests (i.e., reduced and enlarged clutches differ by almost two eggs), there was no difference in the number of eggs hatched or fledglings produced between the three groups.

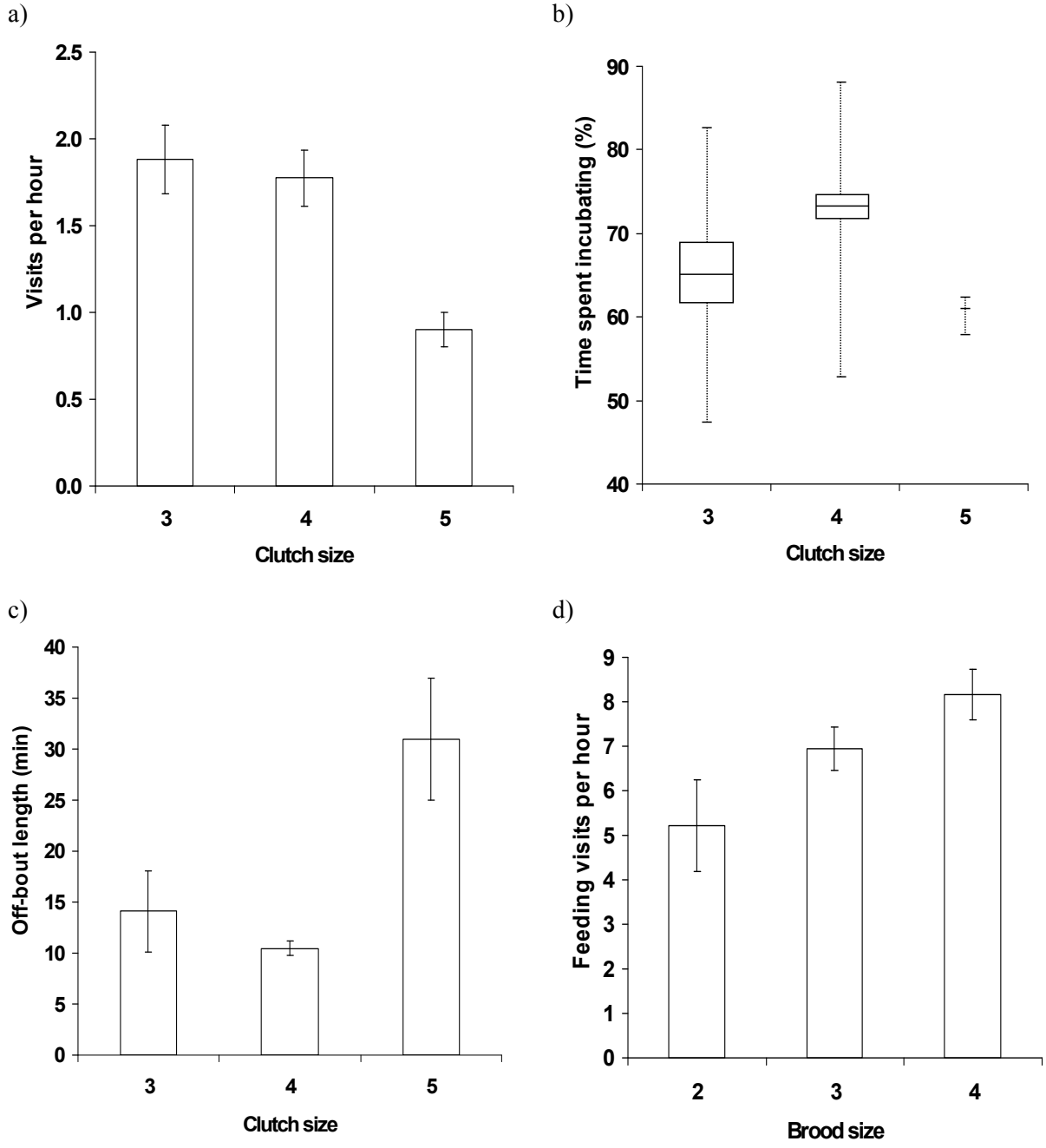

Figure 5.3. Results of film observations (means ± SE): a) number of visits per hour during incubation, b) incubation attentiveness for natural clutch sizes, c) off-bout length (mean time between incubation bouts, here given in minutes), and d) number of feeding visits per hour for nests with nestlings at pin break. Visitation rates during incubation were significantly lower and off-bout length significantly higher for clutches of five eggs, while the time spent incubating (note the considerable variation between females) was highest for 4-egg clutches and lowest for 5-egg clutches.

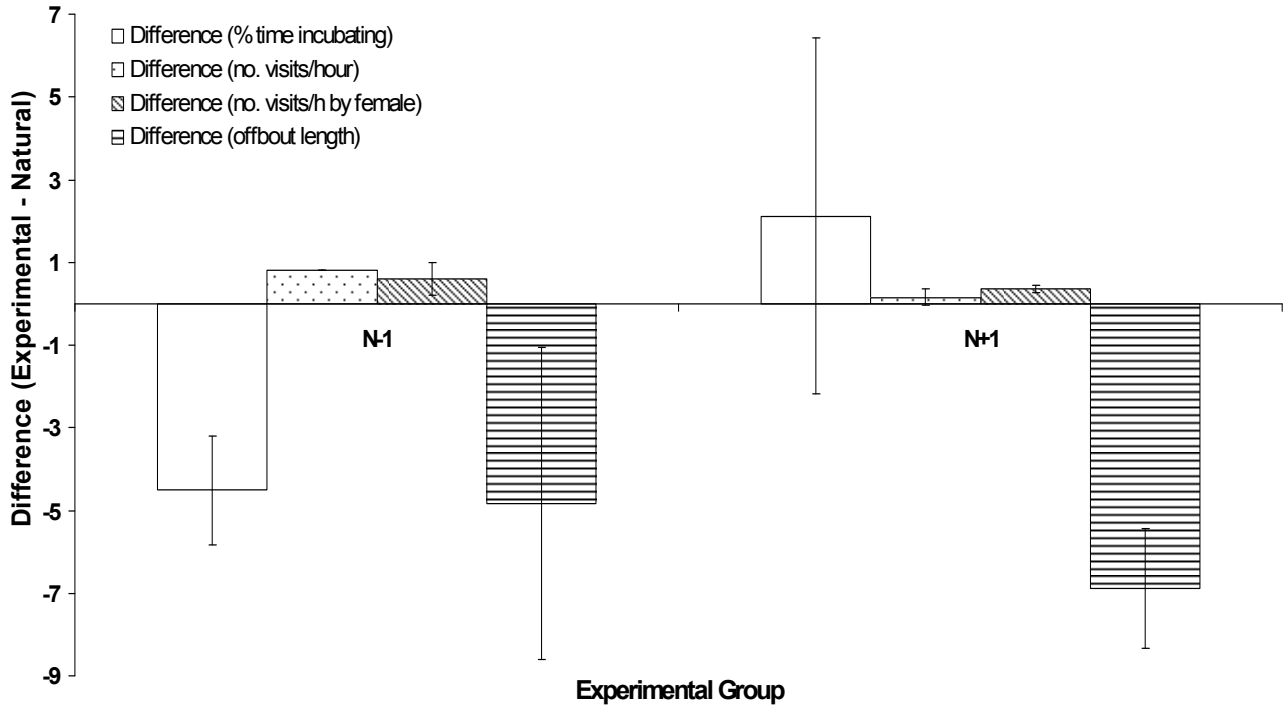

Figure 5.4. Mean difference (± SE) in incubation attentiveness (unshaded bars), number of visits per hour (dot-shaded bars), number of visits by the female (diagonally-shaded bars) and off-bout length (horizontally-shaded bars) for the repeated filming of reduced (N-1) and enlarged (N+1) clutches (one film was of the nest with its natural clutch, the other was of either an experimentally reduced or enlarged clutch). There was no significant difference in incubation attentiveness, though there was a trend for decreased attentiveness with reduced clutches. Visitation rates and off-bout length (mean time between incubation bouts, here given in minutes) were significantly higher for nests when they contained enlarged clutches. Hence, the experiment did modify female behaviour but females did not respond by changing incubation attentiveness.

=== Chapter 6 ===

General Discussion

The clutch size of song thrushes (*Turdus philomelos*) appears to have decreased rapidly after their introduction to New Zealand, so that within 80 years it was already smaller than in the native range. Other life-history traits have also changed since their introduction: song thrush eggs are now significantly smaller and more pointed, and the incubation period more than a day longer in New Zealand, which suggests that there has also been a reduction in investment in egg production and incubation effort. The nestling period of song thrushes was also significantly shorter by about half a day, and both the number of successful nests and the proportion of fledglings produced per nest were significantly lower than in the native range. Although I was not able to measure the extent of post-fledging care and subsequent offspring survival, overall investment in each breeding attempt appears to be lower in New Zealand than in European populations of song thrushes. Furthermore, the high number of successful nests subject to brood reduction (29%) suggests that many pairs may be limited by food availability, as rainfall is lower in many parts of their introduced range.

The link between environmental condition and productivity appears to provide an explanation for the decrease in clutch size of New Zealand thrushes. My results suggest that selection is currently acting against large clutches (at least at Kowhai Bush), especially clutches of five, which are rare in New Zealand but common in Britain. Even clutches of four, the most common clutch size in both New Zealand and Britain, produced fewer young in New Zealand. On average, thrushes that laid clutches of three eggs produced the same number of fledglings as 4-egg clutches, thus many females laying four eggs gained no benefit from the extra egg, despite paying the additional costs of producing and incubating an extra egg. The change in latitude (and environmental conditions correlated with latitude) from Britain to New Zealand may have reduced the ability of parents to provision the large broods that are common in the native range, and favoured a reduction in clutch size.

Many scientists have little interest in introduced species, seeing them as undesirable or irrelevant additions to the native biota. Yet introduced species provide a unique opportunity to study

how animals adapt to novel environments; they are species that have managed to survive and reproduce in environments that often differ in measurable ways from their former, native range, and as a result, are likely to be experiencing strong directional selection pressure in their new range. This process is evident in New Zealand: since their introduction, song thrushes have undergone a rapid decrease in clutch size that my results suggest is adaptive. Some of the changes in environmental conditions experienced by thrushes since their introduction may be analogous to many changes experienced by native species that are affected by habitat modification or competition with introduced species. Studying introduced species is therefore useful both for learning more about evolutionary processes and for applying that knowledge to assist in the conservation of native species that are facing or might come to face similar selection pressures in the future.

All introduced species pass through a bottleneck, which could affect the genetics of post-bottleneck populations and cause reduced reproductive success via inbreeding depression (lower fitness as a result of breeding between related individuals or reduced genetic variation; Frankham *et al.* 2002). However, as a relatively high number of song thrushes (~400 individuals) was released in a short period of time (>250 in two years) during their introduction to New Zealand (Thomson 1922, Long 1981), it is unlikely that inbreeding depression among the founding individuals is responsible for the changes in life-history traits between the native and introduced populations. For example, Briskie & Mackintosh (2004) found that only bottlenecks of <150 individuals resulted in inbreeding depression that caused significantly higher levels of hatching failure compared with the source population. Furthermore, the range of clutch sizes observed in New Zealand is the same as that for the source (British) population (2-6 eggs, with rare cases of one and seven eggs), suggesting that the full range of genetic variation in clutch size is present in both the source population and the introduced population. If birds laying larger clutches had higher fitness in New Zealand, one might expect that the proportion of larger clutches would have increased in the population regardless of the initial ratios, but this is not the case.

My clutch- and brood-size manipulations suggest that birds at Kowhai Bush cannot raise more offspring than the modal clutch size (four eggs), which is contrary to the findings of most brood enlargement experiments (e.g., Lessells 1986, Briskie & Sealy 1989, Martin 2002, Dobbs *et al.* 2006). At Kowhai Bush, clutches of four eggs (modal size) were not significantly more productive than

clutches of three eggs, which actually suggests that 3-egg clutches are optimal in this population. However, 4-egg clutches appear to be more productive in other areas, as data from throughout New Zealand (the OSNZ nest records) showed that the number of fledglings significantly increased with clutch size from two to five eggs. The productivity of different clutch sizes may vary between regions, and this is could be responsible for differences in mean clutch size between regions. The data from OSNZ nest records were not sufficient to assess whether the region in which a certain clutch size was most common (out of all the other regions) was also the region in which that clutch size was most productive, but a comparison of the proportions of each clutch size in each region suggested that this may be the case. On the other hand, high quality habitats may increase the productivity of all clutch sizes. For example, Region 4 (south-eastern North Island, Chapter 3, Fig. 3.1) produced the highest number of fledglings for all clutches except 5-egg clutches, which produced the most fledglings per clutch in Region 3 (south-western North Island). However, low sample sizes expose these data to the greater influence of chance events (i.e., means/probabilities can be skewed due to low numbers), so no firm conclusions can be gathered from differences in proportions. Focused studies of populations in each region would be valuable to further access the productivity of thrushes in each region, and whether selection favours smaller or larger clutches in different habitats, as well as the factors affecting song thrush productivity.

One possible reason for differences in productivity, both within New Zealand and between New Zealand and Britain, is differences in food availability. Latitude can be a broad indicator of both climate (lower latitudes are generally warmer and less seasonal than high latitudes) and the amount of time available for foraging (i.e., the hours of daylight) and these two factors can have a significant effect on food supply (Lack 1947, Martin 1987, Evans *et al.* 2005). Clutch size and body size have both decreased in line with the difference in latitude between New Zealand and Britain (clutch size: Chapter 3, body size: Murphy 1985), but there was no significant effect of latitude within New Zealand. However, rainfall may also affect food availability for thrushes, and as patterns of rainfall do not vary consistently with latitude, this may mask any underlying latitudinal effect within New Zealand. Given the nature of the song thrush diet, quantifying food availability is difficult as they can forage over long distances and exploit both fruit and soil invertebrates (Cramp 1988). Earthworms are their preferred prey (especially for feeding nestlings) and as these animals move deeper into the soil as

it dries out (Gerard 1967), making them less accessible to birds, rainfall may be the best indicator of food availability.

Using the OSNZ nest record database, I found that mean clutch size significantly increased with rainfall, which may be related to differences in food availability (at least the availability of earthworms is likely to be higher in regions with higher rainfall). Reproductive success was also significantly related to climate. Both fledging success and nest success decreased significantly with hours of sunshine, while the mean number of eggs hatched per nest decreased with temperature, but unlike fledging success, did not differ between city regions within New Zealand. This suggests that differences in reproductive success are the result of differences in the ability of parents to successfully fledge all their young, which supports the idea that food availability during the nestling period is both limited by rainfall and lower in New Zealand than in Britain. Hence, differences in clutch size may be the result of food limitation during the breeding season in New Zealand, which has led to changes in reproductive strategies (Martin 1987). The high rates of brood reduction (29% of successful broods), which are unusual for this species (Lack 1949, Kelleher & O'Halloran 2006), suggest that selection is still acting against large clutch size in this population. Hõrak *et al.* (1997) found higher rates of brood reduction in an urban population of great tits (*Parus major*) than in a woodland population and proposed that the cause was immigration from areas where large clutch sizes were not selected against. It is possible this is also occurring at Kowhai Bush, though movements of birds post-fledging and throughout their lives have not been studied in sufficient detail to confirm this.

Female quality or condition may have important effects on life-history traits, so variation in reproductive traits may be sustained via different individuals having different optima ('individual optimisation'; e.g., Pettifor *et al.* 2001). Evidence for this hypothesis is unequivocal (e.g., Nur 1986, Tinbergen & Both 1999, Torok *et al.* 2004), and clutch size at Kowhai Bush is still commonly larger than the number of offspring pairs can raise, despite the decrease that has occurred, so either this trait is not matched to individual ability or other factors are currently more important (e.g., environmental conditions). Nevertheless, individuals that succeeded in fledging four offspring likely had higher fitness than those fledging only three offspring, and my data suggest that differences between females do affect reproductive success. Although I did not measure female condition directly, nest size was significantly related to both absolute and relative levels of success and nests with larger inner volumes

were also less likely to be abandoned. As nest construction is carried out by females alone and larger nests are probably more costly to build (examples from other species: Tomás *et al.* 2006, Mainwaring & Hartley 2009), this suggests that females in better condition (or of genetically high quality) both built nests with larger inner volumes and had higher reproductive success. Experiments involving changing female condition (e.g., food supplementation or watering the territory) may be useful to tease apart the effect of individual quality and how that influences the amount of investment in nest building and the effect of selection on the entire population (e.g., is predation selecting for particular nest characteristics?).

Egg size is highly heritable, but female quality and age have also been found to influence the size of a female's eggs (Ardia *et al.* 2006). While I found hatchling size and egg size were related, I found no significant effects of egg volume on the other fitness traits I measured (hatching success, brood reduction and fledging success). Thus reduced investment in the egg stage does not appear to be having an effect on offspring quality. Briskie & Macintosh (2004) found that hatching failure rates were significantly higher in New Zealand than in Britain, but hatching success at Kowhai Bush was not significantly different, so the observed decrease in egg size is apparently not sufficient to have a negative effect on hatching success. In fact, no negative effects of egg size on offspring fitness were found, and the high rates of nest failure (65%) may make laying slightly smaller eggs (and smaller clutches) adaptive (Slagsvold 1984), though this cannot be confirmed from this study. Many studies make no attempt to measure egg size as part of the normal range of life-history traits included in basic studies of breeding biology, yet it provides useful information additional to clutch size and requires minimal additional disturbance or effort once a nest is located.

Egg shape of song thrushes in New Zealand was also significantly different from the source population, with an increase in the elongation of the egg (i.e., eggs are more pointed). However, unlike the difference in egg volume, my results suggest that the change in egg shape has had a negative effect on offspring condition, so differences in egg shape may be a non-adaptive consequence of lower female condition or smaller body size. Hõrak *et al.* (1997) found that great tits laying large eggs had higher fitness, as more of their offspring survived to breed, and they proposed that female quality was causing the apparent correlation between egg size and survival. In the song thrush population at Kowhai Bush, female quality may also be more important than egg morphology *per se*. Nests

containing more pointed eggs were given lower levels of incubation, potentially had lower hatching success, and experienced more instances of brood reduction than nests with more rounded eggs, despite within-clutch differences in egg size and shape not being related to hatching success. Assuming that low levels of incubation provide a poorer-quality environment for embryo development and that females in better condition are able to incubate for longer and provide more food to their nestlings (e.g., Thomson *et al.* 1998, Hanssen *et al.* 2003, Dobbs *et al.* 2006), these differences suggest that females laying more pointed eggs were of lower quality. Egg shape is thought to be mainly caused by a combination of the shape of the female's pelvis and muscular activity (Romanoff & Romanoff 1949, Deeming 2002), so lower-quality females may be structurally different, or less able to control muscular action in the oviduct. Measurements of adult thrushes at Kowhai Bush (e.g., body mass and tarsus length) are necessary to link egg size and shape with female quality, though the high risk of nest desertion precluded me from collecting such data in this study. Perhaps a future study concentrating on egg morphology and female condition, measured within days of clutch completion, could provide that information, while eggs could be collected and their contents and shell properties also measured, to further elucidate egg quality and female quality.

6.1 Future research

My survey of life-history traits in New Zealand song thrushes revealed a variety of differences between the introduced and native populations. I was only able to examine a few of the traits in detail and there is wide scope for more depth and experimental approaches to determine the underlying causes for these differences. For example, it is unclear why the incubation period is now longer in New Zealand, yet the nestling period is shorter. Data on incubation attentiveness and feeding rates in the native range would be useful for comparison, but more detailed studies could also be carried out within New Zealand to determine what factors are driving these changes. Similarly, I found that adult body size has decreased in New Zealand, but have no explanation for this change beyond finding that the change follows the expected latitudinal pattern (Murphy 1985), and latitude itself is only the proxy for whatever environmental factor(s) is selecting for smaller body size. The breadth of changes that has occurred in New Zealand song thrushes, coupled with the rapidity and recentness of the changes,

provides an ideal opportunity to study selection on life-history traits in a way not possible in a species' native range, where most selection is expected to be stabilising.

The importance of food limitation relative to other factors that may affect clutch size and other life-history traits, such as nest predation, could be teased apart using large-scale experiments aimed at increasing nest success and/or increasing food availability. For example, nest predation rates could be manipulated by trapping predators in an area such as Kowhai Bush, or utilising the areas inside predator-proof fences, would enable comparisons of clutch size between areas of high and low predation risk. Manipulating food availability between regions with high and low predation could then be used to determine how food limitation interacts with nest predation to select for changes in clutch size. As song thrushes appear reliant on moist leaf litter for locating preferred food sources, artificially increasing rainfall via irrigating sections of the habitat, or some territories, could be used to increase food availability, which could then be used to assess levels of reproductive success and brood reduction. Undertaking brood enlargement experiments under these manipulated environmental regimes would also be useful to determine whether pairs are able to feed more offspring when food availability has been increased.

Even for life-history traits I have studied in depth, there is a need for further data. Because rates of nest failure and hatching success are both high (~90% of eggs that survived to hatch did so, which is typical of most bird species), I had few measurements of unhatched eggs; thus, more data on the morphology of unhatched eggs are also required. Transferring eggs between nests would also assist in distinguishing between female/parental quality and the effects of specific traits on offspring survival and condition. Data on egg mass loss rates over the entire incubation period would also be useful to determine whether incubated, unhatched eggs lose more mass than hatched eggs, as my limited data on this question suggest that mean mass loss was higher for nests containing one unhatched egg than for nests in which all eggs hatched. Rates of egg mass loss may vary in relation to climatic conditions, so data from a 'wet' region would provide a useful comparison with the rates observed at Kowhai Bush, a 'dry' region. Studies of egg size in different areas could also determine whether changes have occurred throughout New Zealand. Flux (1966) found a decrease in the size of song thrush eggs in a population at St. Arnaud (42ºS, near Kowhai Bush), and the mean volume (5.66 cm^3), based on eggs from 43 clutches, was similar to the mean for Kowhai Bush (5.60 cm^3, Chapter 4). However, Flux

(2006) proposed that the decrease was an artefact of 4-egg clutches containing smaller eggs and being more prevalent than 5-egg clutches. As I found no difference in egg size between different clutch sizes, with a slight trend for 4-egg clutches to contain the largest eggs, this suggests that some populations may be experiencing different selection pressures or, if the decrease in egg size is a consequence of the decrease in body size, that adult size is larger in some areas of New Zealand. Song thrushes have been introduced to other countries (e.g., Australia), so it is also possible to compare life-history traits among multiple introduced populations to determine if similar changes have occurred separately in these populations.

The changes I have found in life-history traits of New Zealand thrushes may be a reflection of plastic or genetic variation in traits, but a study of thrush genetics and the heritability of different traits is required to know for certain. Alternatively, plasticity in traits could be measured using experiments which modify environmental conditions, such as food availability and nest failure rate, to determine whether birds can respond to increased habitat quality in ways that optimise their fitness. Tradeoffs between traits at Kowhai Bush were not clearly apparent in my data (i.e., few traits were related to clutch size); however, the effects of certain tradeoffs may be reflected by my data. For instance, adults may be living longer in New Zealand and this may have selected for the observed reduction in investment per breeding attempt by reducing the value of each attempt (because more attempts can be made). Also, the breeding season may be longer in New Zealand (Evans *et al.* 2005), which would provide additional opportunities to made extra attempts, though this was not the case for the population at Kowhai Bush. As the majority of pairs do not begin breeding until September, there was no observed peak in clutch size before the typical seasonal decline, unlike other areas of New Zealand and in British populations, where breeding is already underway by mid-late winter.

6.2 Conclusion

Rapid evolutionary change punctuated by periods of relative stasis may be the most common pattern of evolution experienced by all species (Grant & Grant 2002, Carroll *et al.* 2007). In New Zealand, clutch size of song thrushes decreased within 80 years (<30 generations) of their introduction, and selection may even be favouring further reductions. Although my study was focused on a non-endangered, introduced bird that most conservation biologists would consider a pest, the ways in

which such species adapt to novel selection pressures could provide important insights for the conservation of native species. For example, a better understanding of how environmental change affects life-history traits could be useful in predicting which species/populations may be at risk before population declines occur, as well as help in developing the most effective methods for population recovery. Introduced birds may be a model system for this type of study, as non-endangered, natural populations are probably not experiencing the same sort of strong directional selection that may be felt by many endangered species. For example, habitat modification and the introduction of exotic predators has likely placed intense selection pressure on many native New Zealand birds. Some, like the bellbird (*Anthornis melanura*), appear to be changing some life-history traits in response to this novel selection pressure (Massaro *et al.* 2008). Thus there is a clear need to better understand which life-history traits can change, the speed at which they can change, and which traits seem resistant to change. Such information is becoming more urgent as human-effected environmental change, including climate change, continues to modify natural habitats around the world. In the current era of global climate change, many species that were experiencing stabilising selection (i.e., those displaying the extremes of a certain trait are selected against and the average value favoured) may now be experiencing directional selection, such that the majority of individuals do not possess the favoured characteristic(s). If these individuals are unable to make plastic changes to adapt, their rates of survival and/or reproduction are likely to be negatively affected.

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